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1987

VOLUME I

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The Diet of Widow Rockfish *Sebastes entomelas* in Northern California

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ABSTRACT

The diet of widow rockfish (*Sebastes entomelas*) taken in the commercial and partyboat fisheries from Northern California was examined. The only sampling category that had sufficient numbers to be reliable was the commercial catch from the Eureka area. The diet of these fish is dominated by four prey categories: salps; fish, primarily myctophids; caridean shrimp, almost exclusively *Sergestes similis*; and euphausiids. There is a seasonal trend in the composition of these four prey categories which corresponds with their life history. There are also size related trends in diet composition. These four major prey groups comprise the deep sounding layer. At night when the widow rockfish are caught at depths of around 140 m, the deep sounding layer is near the surface. This suggests that the widow rockfish is feeding during the day when the deep sounding layer is in deeper waters (400 m). The strong similarity between widow rockfish and blue rockfish (*Sebastes mystinus*) is pointed out, which suggests strong parallel forces are important in the evolution of both of these species.

INTRODUCTION

With the exception of nearshore species, very little work has been done on the feeding of rockfishes (Genus *Sebastes*). The only information available on commercially important rockfishes in California are comments by Phillips (1964) in his report on age and growth. In that paper he states, "The widow rockfish is mainly a macroplankton feeder, with hyperiid amphipods dominating their diet, but small fish are also eaten at times." From this he concludes that "Since amphipods are seldom found in the diet of other macroplankton-feeding rockfish, the widow rockfish might occupy a somewhat different habitat." In these comments and those on the relatively pure nature of widow rockfish commercial catches, Phillips makes the suggestion that the feeding behavior of the widow rockfish is radically different from other commercially important species of rockfish. This possibility warrants more detailed examination in light of the recent dramatic increase in the importance of the widow rockfish in the commercial fishing industry from San Francisco northward (Demory 1987; Quirollo 1987; Tagart 1987).

METHODS

The stomachs of widow rockfish were sampled from both commercial and partyboat catches at ports between Eureka and Monterey. From each catch a maximum of 20 fish was sampled. The sampling began March 1980 and continued until February 1981. All fish lengths used in this paper are total lengths. The digestive tract of each fish specimen was removed and preserved in 4% formaldehyde solution. For analysis, the contents were examined under a binocular dissecting microscope and, when necessary, a binocular compound microscope. A list was then compiled of the items in the gut, with species identified whenever feasible. The following data were then noted for the items in each listed category: 1) the number present; 2) prey size range; and 3) an estimate of its representation in the gut as a percent by volume of the contents. Empty stomach samples were excluded from the data.

RESULTS

Most of the stomach samples (74% or 283/381) of widow rockfish came from commercial catch sampling in the Eureka-Fields Landing area. This is the only sampling category that had sufficient numbers to be reliable. These samples came predominantly (over 75%) from the same California Department of Fish and Game statistical block just south of Cape Mendocino. The diet item with the largest mean percent volume (the average for any one prey category of its percent volume from all non-empty fish) was thaliacean urochordates or salps (Table 1). Salps are gelatinous herbivorous holoplankton which have the capacity for rapid population increase due to high growth rates and short generation time (Blackburn 1979). Because of this, they are considered opportunistic species, able to quickly produce large formations when high concentrations of food become available. Almost equally important in the diet are fish, which when identifiable are usually myctophids or Pacific hake. Myctophids are small fish with photophores which give off bioluminescence. They are probably the most common fish in midwater (Paxton 1967). Pacific hake (*Merluccius productus*) is a semipelagic fish extremely abundant off the coasts of California, Oregon, and Washington. The hake found in widow rockfish stomachs are all in the size range of age-1 fish or younger (Dark

Table 1—Diet of widow rockfish from catch samples landed in the Eureka-Fields Landing area. (Average TL = 467 mm, *n* = 283, min. size = 370 mm, max. size = 795 mm).

	Mean number	Mean % volume	Mean prey size (mm)	Freq. of occurrence
Hydromedusae				
Unid. sp.	0.01	0.017	—	0.004
Physonectid siphonophore	0.22	1.359	11.00	0.028
Ctenophora				
Pleurobrachia bachei	0.13	0.836	20.63	0.018
Oligochaeta				
Unid. sp.	—	0.042	90.00	0.004
Polychaeta				
Alciopidae	0.01	0.408	—	0.007
Heteronereis sp.	0.09	0.428	26.00	0.004
Gastropoda				
Unid. sp.	0.07	0.491	1.50	0.018
Turridae	0.07	0.038	—	0.004
Vermiculuridae	0.07	0.428	—	0.004
Cephalopoda				
Unid. sp.	0.15	0.352	181.00	0.028
Loligo opalescens	0.02	0.338	46.25	0.007
Octopus sp.	0.01	0.193	33.50	0.007
Mysidacea				
Unid. sp.	0.01	0.022	10.00	0.004
Isopoda				
Jaeropsis sp.	0.01	0.428	12.50	0.004
Gammaridea				
Unid. sp.	0.06	0.587	2.80	0.028
Hyperiidae				
Unid. sp.	0.57	1.281	70.38	0.109
Phronimidae	0.02	0.095	26.25	0.007
Vibilliadae	0.73	0.639	36.00	0.085
Caprellidea				
Unid. sp.	—	0.008	35.00	0.004
Euphausiacea				
Unid. sp.	27.36	17.759	49.86	0.325
Unid. larvae	3.53	0.428	—	0.004
Euphausia pacifica	0.02	0.428	24.50	0.004
Thysanoessa spinifera	—	0.013	—	0.004
Natantian Decapoda				
Unid. sp.	5.14	9.513	30.94	0.102
Unid. megalopa	0.01	0.150	10.00	0.007
Caridea	—	0.428	—	0.004
Pandalus jordani	0.01	0.107	—	0.004
Sergestes similis	8.44	11.600	27.75	0.166
Thaliacea				
Unid. sp.	14.87	25.332	131.07	0.329
Larvacea				
Unid. sp.	0.14	0.008	4.50	0.004
Chaetognatha				
Unid. sp.	—	0.428	35.00	0.007
Sagitta sp.	—	0.408	—	0.004
Fish				
Unid. sp.	0.05	10.045	124.84	0.113
Mustelus henlei	0.05	0.034	22.50	0.004
Engraulis mordax	0.02	1.029	60.00	0.004
Myctophidae	6.01	5.513	37.46	0.152
Lampanyctus ritteri	—	0.215	60.00	0.004
Tarletonbeania crenularis	0.02	1.221	63.25	0.014
Merluccius productus	0.14	6.812	114.07	0.060
Aulorhynchus flavidus	—	0.086	56.00	0.004
Anoplopoma fimbria	—	0.428	—	0.004
Mycteroperca jordani	0.03	0.019	27.50	0.004

1974). Data on age-1 fish suggest that they are almost completely segregated, even from age-2 fish (J. Taynor, Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Serv., NOAA, unpubl. data). Hake spawn from February to April, peaking in March (Ahlstrom and Counts 1955). In the January-March quarter, hake appear in the diet of widow rockfish both as young-of-the-year fish and 1-yr fish. Hake then virtually disappear from the diet until the October-December quarter when they are the major item. Caridean shrimp, almost all those identifiable being *Sergestes similis*, account for another 22% of the diet. The final major prey category of the widow rockfish is euphausiid crustaceans which comprise about 19% of the diet.

These prey types represent about 91% of the diet of widow rockfish, again in terms of volume. The stomach contents of an individual averaged 1.8 different types of prey per stomach. There are virtually no hyperiid amphipods (1.25%) in the widow rockfish's diet, and most of those which are identified (Vibilliadae 0.95%) are from a genus that has been reported as living in association with salps (Madin and Harbison 1977). In fact, these data are pretty much in direct contradiction with Phillips' description of the widow rockfish's diet of "primarily hyperiid amphipods, occasionally salps, pyrosomes, small squid and anchovies." This contradiction may be due to difference in location of fish capture and to differences in sample sizes.

Seasonality in the diet of widow rockfish was examined through quarterly diets (Jan.-Mar., Table 2; Apr.-June, Table 3; July-Sept., Table 4; Oct.-Dec., Table 5). Average size of fish was similar for all quarters (range 449 to 487 mm), but samples were small for some quarters. The four major groups mentioned above account for between 73 and 97% of the quarterly diet volumes (versus 91% for the annual diet), but the distribution of diet volume during the quarters is different among these groups. In the winter quarter, shrimp, primarily sergestids, are an important part of the diet. This was true both in 1980 and 1981. The seasonal occurrence of these prey may be due to an onshore migration during this period (Pearcy and Forss 1966a). The spring quarter (April through June) is the only time that salps are a major part of the diet. This is also the period of high absolute volume of prey per millimeter of fish size and highest number of prey species per fish, but neither is statistically significant. The diet information from the summer quarter is limited by sample size, but during this period euphausiids dominate the diet. During the fall, fish is the principal prey item, particularly juvenile hake.

To investigate possible changes in feeding with size, the widow rockfish from Fields Landing are broken down into three size classes: <450 mm, 450-500 mm, and >500 mm. The two major trends in diet with increasing fish size are the decreasing importance of euphausiids and a corresponding increase of fish in the diet (Table 6). The increase of fish is greater than the decrease in euphausiids, but there is also a slightly increasing trend in salps with larger fish size. Prey size generally increases as the fish size-class increases, with the exception of shrimp. The larger fish come from several collections spread over different months, so it is not likely that these changes are simply a sampling artifact.

There are numbers of fish collected from May and June at each of the three southern areas: Fort Bragg, San Francisco, and Monterey. Average sizes of fish from these three areas are within 100 mm of those from Eureka. In the Fort Bragg samples (Table 7), which are commercially caught, the diet is predominantly salps. In San Francisco Bay (Table 8), where the samples are sport-caught, the diet is predominantly euphausiids. In Monterey, where the samples are a mixture of commercial and sport-caught fish, the diet is a mixture of salps and euphausiids (Table 9). Fish and shrimp are virtually absent from these samples.

Table 2—Diet of widow rockfish from Eureka, January-March 1981. (Average TL = 487 mm, *n* = 32, min. size = 419 mm, max. size = 795 mm).

	Mean number	Mean % volume	Mean prey size (mm)	Freq. of occurrence
Hyperiidea				
Paraphronima sp.	5.63	3.215	32.50	0.063
Euphausiacea				
Unid. sp.	0.44	3.723	13.75	0.094
Natantian Decapoda				
Unid. sp.	19.13	27.074	31.43	0.250
Sergestes similis	23.88	35.159	30.91	0.375
Thaliacea				
Unid. sp.	0.19	3.723	20.00	0.063
Fish				
Unid. sp.	0.03	2.031	25.00	0.094
Merluccius productus	1.13	1.558	36.25	0.156
Myctophidae	0.22	23.518	118.00	0.219

Table 3—Diet of widow rockfish from Eureka, April-June 1980. (Average TL = 467 mm, *n* = 176, min. size = 390 mm, max. size = 528 mm).

	Mean number	Mean % volume	Mean prey size (mm)	Freq. of occurrence
Ctenophora				
Pleurobrachia bachei	0.22	1.342	20.63	0.028
Oligochaeta				
Unid. sp.	0.01	0.069	9.00	0.006
Gastropoda				
Unid. sp.	0.03	0.079	1.50	0.017
Turridae	0.11	0.062	—	0.006
Vermiculuridae	0.11	0.688	—	0.034
Cephalopoda				
Unid. sp.	0.23	0.544	65.00	0.034
Loligo opalescens	0.02	0.516	52.50	0.006
Octopus sp.	0.01	0.275	55.00	0.006
Isopoda				
Jaeropsis sp.	0.01	0.688	12.50	0.006
Gammaridea				
Unid. sp.	0.10	0.254	2.80	0.045
Hyperiidae				
Unid. sp.	0.48	0.164	15.81	0.091
Phronimidae	0.03	0.151	26.25	0.011
Vibilliadae	1.15	0.971	15.43	0.114
Caprellidea				
Unid. sp.	0.01	0.013	35.00	0.006
Euphausiacea				
Unid. sp.	42.11	22.101	15.50	0.415
Unid. larvae	5.68	0.688	—	0.006
Natantian Decapoda				
Unid. sp.	4.78	9.763	30.76	0.119
Unid. megalopa	0.01	0.172	10.00	0.006
Caridea	—	0.688	—	0.006
Sergestes similis	9.19	10.642	26.11	0.188
Thaliacea				
Unid. sp.	23.20	37.019	158.21	0.472
Fish				
Unid. sp.	0.35	4.527	26.67	0.142
Mustelus henlei	0.08	0.054	22.50	0.006
Myctophidae	9.46	8.530	37.62	0.216

Table 4—Diet of widow rockfish from Eureka, July-September 1980. (Average TL = 449 mm, *n* = 27, min. size = 374 mm, max. size = 506 mm).

	Mean number	Mean % volume	Mean prey size (mm)	Freq. of occurrence
Hydromedusae				
Unid. sp.	0.07	0.257	—	0.037
Physonectid siphonophore	0.11	1.285	—	0.037
Gastropoda				
Heteropod	0.56	6.423	—	0.037
Cephalopoda				
Loligo opalescens	0.11	0.257	40.00	0.037
Mysidacea				
Unid. sp.	0.11	0.321	10.00	0.037
Hyperiidae				
Unid. sp.	2.59	18.175	9.50	0.360
Vibilliadae	0.11	0.513	7.50	0.111
Euphausiacea				
Unid. sp.	3.93	46.564	20.00	0.444
Euphausia pacifia	0.22	6.423	24.50	0.037
Natantian Decapoda				
Pandalus jordani	0.11	1.606	—	0.037
Thaliacea				
Unid. sp.	0.44	1.477	—	0.740
Fish				
Unid. sp.	0.08	3.853	—	0.037
Anoplopoma fimbria	0.04	6.423	—	0.037
Merluccius productus	0.04	6.423	—	0.037

Table 5—Diet of widow rockfish from Eureka, October-December 1980. (Average TL = 465 mm, *n* = 48, min. size = 370 mm, max. size = 531 mm).

	Mean number	Mean % volume	Mean prey size (mm)	Freq. of occurrence
Hydromedusae				
Physonectid siphonophore	1.21	7.296	11.00	0.146
Polychaeta				
Alciopidae	0.04	2.333	—	0.042
Gastropoda				
Unid. sp.	0.02	0.074	—	0.021
Cephalopoda				
Unid. sp.	0.04	0.074	13.00	0.042
Octopus sp.	0.02	0.123	12.00	0.021
Hyperiidae				
Unid. sp.	0.14	0.467	4.33	0.104
Vibilliadae	0.02	—	5.00	0.021
Euphausiacea				
Unid. sp.	4.42	2.333	12.50	6.083
Thysanoessa spinifera	0.02	0.074	—	0.021
Natantian Decapoda				
Sergestes similis	0.13	2.948	32.50	0.042
Thaliacea				
Unid. sp.	2.21	9.702	18.42	0.125
Larvacea				
Unid. sp	0.83	0.050	4.50	0.021
Chaetognatha				
Unid. sp.	—	2.456	—	0.021
Fish				
Unid. sp.	1.14	38.442	35.00	0.542
Engraulis mordax	0.10	5.895	60.00	0.063
Lampanyctus ritteri	0.02	1.228	60.00	0.021
Tarletonbeania crenularis	0.13	7.001	63.25	0.083
Merluccius productus	0.69	19.503	104.25	0.188

Table 6—Diet of widow rockfish broken down into size classes from Eureka-Fields Landing area using only major prey categories.

	Mean number	Mean % volume	Mean prey size (mm)	Freq. of occurrence
Widow rockfish <450 mm (Avg. TL = 435 mm, *n* = 89)				
Fish	1.98	18.272	51.60	0.161
Euphausiids	67.10	21.554	17.50	0.301
Shrimp	10.56	13.288	41.22	0.277
Salps	6.90	19.560	27.50	0.313
Widow rockfish 450-500 mm (Avg. TL = 473 mm, *n* = 186)				
Fish	7.95	22.322	46.55	0.304
Euphausiids	17.98	14.785	63.63	0.352
Shrimp	16.00	22.414	37.67	0.296
Salps	18.29	22.987	41.00	0.333
Widow rockfish >500 mm (Avg. TL = 512, *n* = 29)				
Fish	1.05	32.264	76.66	0.385
Euphausiids	2.93	6.857	50.00	0.069
Shrimp	12.96	19.668	45.84	0.241
Salps	22.76	29.159	45.00	0.379

Table 7—Diet of widow rockfish from the Fort Bragg area. (Average TL = 457 mm, *n* = 28, min. size = 380 mm, max. size = 524 mm).

	Mean number	Mean % volume	Mean prey size (mm)	Freq. of occurrence
Hydromedusae				
Calycophoran siphonophore	0.04	0.781	30.00	0.036
Gammaridea				
Unid. sp.	0.04	0.039	—	0.036
Hyperiidae				
Vibilliadae	2.04	4.609	4.00	0.250
Euphausiacea				
Unid. sp.	15.29	5.469	7.50	0.179
Thysanoessa spinifera	0.11	0.196	2.50	0.036
Ascidiacea				
Dolioid	0.21	3.125	17.50	0.036
Thaliacea				
Unid. sp.	26.64	82.070	74.00	0.607
Fish				
Sebastes saxicola	0.04	0.781	30.00	0.036

Table 8—Diet of widow rockfish from the San Francisco Bay area. (Average TL = 382 mm, *n* = 20, min. size = 305 mm, max. size = 461 mm).

	Mean number	Mean % volume	Mean prey size (mm)	Freq. of occurrence
Hyperiidae				
Unid. sp.	0.20	1.113	13.50	0.150
Vibilliadae	0.45	4.016	8.50	0.200
Euphausiacea				
Unid. sp.	6.90	70.481	26.57	0.500
Natantian Decapoda				
Sergestid larvae	0.50	5.750	3.50	0.050
Thaliacea				
Unid. sp.	0.50	9.274	15.00	0.050
Gelatinous material, undet.	—	9.274	3.00	0.050
Fish				
Unid. sp.	0.05	0.093	6.00	0.050

Table 9—Diet of widow rockfish from the Monterey area. (Average TL = 436 mm, *n* = 50, min. size = 266 mm, max. size = 557 mm).

	Mean number	Mean % volume	Mean prey size (mm)	Freq. of occurrence
Hydromedusae				
Calycophoran siphonophore	0.02	0.061	4.00	0.020
Physonectid siphonophore	1.56	1.768	21.67	0.100
Gastropoda				
Carinaria japonica	0.04	2.439	70.00	0.040
Isopoda				
Unid. sp.	—	0.030	2.00	0.020
Gammaridea				
Unid. sp.	0.14	0.152	—	0.060
Caprellidea				
Unid. sp.	—	0.061	—	0.020
Hyperiidae				
Unid. sp.	0.10	0.640	6.25	0.080
Vibilliadae	1.56	1.280	4.00	0.100
Euphausiacea				
Unid. sp.	11.72	39.268	10.00	0.380
Decapoda				
Glaucothoe larvae	0.16	3.049	9.00	0.020
Thaliacea				
Unid. sp.	8.60	46.341	57.50	0.420
Fish				
Unid. sp.	0.40	4.695	80.00	0.060
Unid. larvae	0.06	0.152	25.00	0.020
Agonidae	0.02	0.061	19.00	0.020

DISCUSSION

The four major groups—salps, euphausiids, sergestid shrimp, and myctophids—include mostly species reported to be strong vertical migrators (salps - Harbison and Campenot 1979, Wiebe et al. 1979; euphausiids - Brinton 1967; *Sergestes similis* - Pearcy and Forss 1966b; myctophids - Pearcy 1964, Pearcy and Laurs 1966, Paxton 1967). These species comprise the major components of what has been labeled the deep sounding layer. So the principal prey species of the widow rockfish are those that migrate up toward the surface (upper 100 m) during the night and back down into deeper water (400 m) during the day. This means that the widow rockfish is feeding in the upper levels of the water column at night or in deeper water during the day. The commercial fishery operates predominantly at night and makes large, relatively pure catches of widow rockfish exclusively at depths greater than 100 m (Demory 1987; Quirollo 1987; Tagart 1987). There is also evidence that widow rockfish disperse around sunrise and reform during nighttime (Gunderson et al. 1981). These catches from large, tight nocturnal aggregations rule out feeding in the upper levels during the day and indicate that these fishes are feeding either at deeper depths predominantly during the day or crepuscularly on the deep sounding layer during its ascent or descent. The bulk of the stomach samples come from the spring quarter, and this interpretation may be somewhat limited by seasonal feeding patterns. Gunderson et al. (1980) examined a limited number of stomach samples of widow rockfish from nighttime tows when the fish are in schools. They concluded that their data indicated little night feeding by widow rockfish was occurring and that most prey were captured during diurnal periods.

There are major differences in the seasonal diets of widow rockfish, while there is little seasonal variation in abundance of the prey species in plankton collections (Pearcy et al. 1977). Most prey items are at their greatest abundance during the April-June quarter, which is the most intense feeding period. This period directly follows the release of the young larval fish by the adult widow rockfish, at which time fat reserves are traditionally low. Over the range of fish sizes available here, there are some significant changes in diet. Euphausiids are gradually replaced by fish in the diet. This, plus a general increase in size in all diet categories, results in an increase in average prey size with increasing fish size. The results from the geographical data are confounded with the effects of commercial and sport-caught fish. The results are intriguing, but sampling sizes are too small to be reliable.

Most species of rockfish have apparent defense structures, such as strong head spines and large dorsal fins, and live on and/or near-bottom (Phillips 1957). However, the widow rockfish is a member of a group of rockfish species, including most commercially and sport-caught species, which have evolved a streamlined body shape with reduced head spines and a smaller dorsal fin for living high in the water column. This smoother, more fusiform shape plus a smaller head (32.8% of standard length), smaller mouth (13.6%), and a smaller orbit diameter (7.9%), characterize the widow rockfish's unique morphology (Phillips 1957). The other rockfish species which is the most similar (streamlined body, small mouth, eyes and head) is the blue rockfish, *Sebastes mystinus*. This species is traditionally the most important component of the partyboat and skin-diving fishery in central California. The blue rockfish is a near-shore species which is active during the daytime and hides among rocks and algae at night (Ebeling and Bray 1976). The diet of the blue rockfish is also similar to that of the widow rockfish. The principal components are gelatinous plankton (tunicates and scyphozoids), crustaceans (amphipods), and fish (Gotshall et al. 1965). The similarities in morphology and diet of these two species suggests strong parallel forces are important in their evolution.

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SPADELLA PIMUKATHAROS, A NEW BENTHIC CHAETOGNATH FROM SANTA CATALINA ISLAND, CALIFORNIA

Angeles Alvariño

Abstract.—*Spadella pimukatharos* is described and compared with closely related species *Spadella legazpichessi, S. nana,* and *S. schizoptera.* These species are related in part by the structure of the adhesive digital organs. The substratum apparently preferred by *S. pimukatharos* is a sediment rich in fragments of coralline algae.

The genus *Spadella* Langerhans was discussed by Alvariño 1970, 1981b, who summarized the differential characteristics of the species and their world distributions. The species of this genus can be divided into two groups, those with adhesive, digital, hand-shaped organs at the ventral part of the tail segment and those without digital, adhesive organs. Among the species with adhesive digital organs (Alvariño 1981a) are species of two types, which can be divided into two subgroups. In *S. pulchella* Owre, 1963, and *S. hummelincki* Alvariño, 1970, the digital organs are covered by thick tubercular papillae, whereas in *S. schizoptera* Conant, 1895, *S. nana* Owre, 1963, *S. legazpichessi* Alvariño, 1981, and *Spadella pimukatharos,* n. sp., the fingerlike structures are strengthened by thin muscular fibers and each fingertip has a pad of very fine papillae.

The species that are closely related to *Spadella pimukatharos* are *S. schizoptera, S. nana,* and *S. legazpichessi. Spadella schizoptera* inhabits the Bahamas (Conant 1895), Misaki, Japan (Yosii and Tokioka 1939), New South Wales, Australia (Mawson 1944), Cayos Soldier, Florida (Owre 1963), Cayo Gun, Bahamas (Feigenbaum 1976). The records from Japan and Australia are probably erroneous identifications because populations of species of *Spadella* do not extend over such wide areas; their distributions are limited to directly-connected zones. *Spadella nana* inhabits Cayos Soldier, Florida (Owre 1963), Bahamas (Owre 1972); *S. legazpichessi* was obtained at Enewetak, Marshall Islands (Alvariño 1981a). *Spadella bradshawi* Bieri, 1974, from San Diego, California, lacks the hand-shaped fingerlike adhesive organs.

Spadella pimukatharos, new species
Figs. 1, 2

Material.—Holotype (USNM 99379), 5 paratypes (USNM 99380) collected at Fisherman's Cove, Santa Catalina Island, California, 13 Mar 1985.

Diagnosis.—The descriptions of the anatomical features are based both on mature adult specimens (Stage IV of sexual development), and young specimens at Stages I, II, and III of maturity.

The body is opaque, with well developed muscles on the dorsal and ventral sides. Lateral sides are very narrow. No pigment or pigmentation pattern has been observed, although the specimens were examined with a microscope shortly after preservation. The colleague who collected them did not find the specimens pigmented.

Total length of full mature specimens reached 3.0, 3.5, and 3.75 mm, excluding the tail fin. Specimens measure 1.75, 2.0, and 2.5 to 2.75 mm at I, II, and III stages of maturity, respectively. The stages of ma-

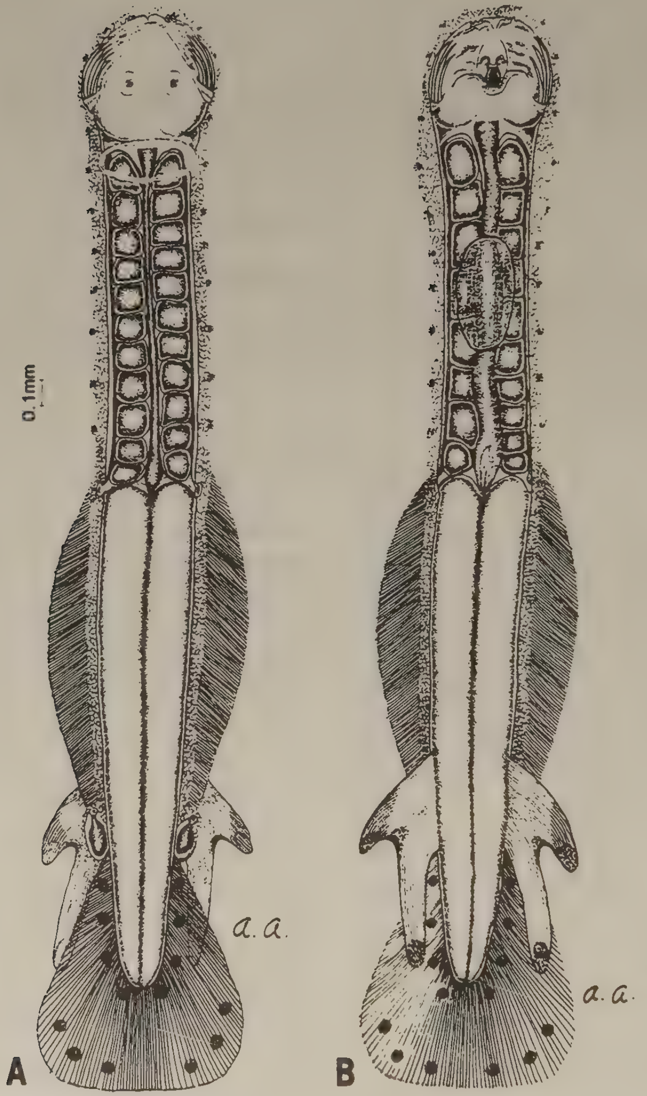

Fig. 1. *Spadella pimukatharos*: A, Dorsal view; B, Ventral view.

turity are based on the development of the gonads, mainly of the ovaries and the ova.

The body is about the same width from head to tail, slightly narrow at the neck and tapering at the end of the tail segment; it widens slightly at the region of the transverse septum that separates the trunk and tail segments.

The head is about as long as wide. Head, trunk, and tail are thickly covered by collarette or alveolar tissue, giving the animal the appearance of having the same width from head to tail, except for the tapering at the end of the tail.

The caudal segment makes up 50% of the total length of the animal.

The eyes are large and roundish, placed at the center of the dorsal side of the head, and are the same distance from each other as from the sides of the head. The pigmented region of the eyes is large and includes 2 branches, the longer branch is parallel to the longitudinal axis of the body, and the short branch extends perpendicularly at midlength from the large branch. The pigment separates 5 small, clear regions filled with lenses: one large region towards the side of the head, 2 small regions toward the center of the head limited by the short and long branches of pigment, and 2 very small regions at the end of the large vertical branch. This general pattern is typical of most chaetognaths.

There are 7–9 hooks at each side of the head. They are thin, curved, and in all examined specimens appeared to be pleated together at the sides of the head. There are 2 to 3 anterior teeth, which are thin, short and pointed. No posterior sets of teeth were observed.

The mouth is on the ventral side, has 2 round pads anterior to it (Fig. 1B).

The corona ciliata, located at the dorsal side of the neck, is ellipse-shaped, with the transverse axis more than twice the length of the vertical axis (Fig. 2A).

The collarette extends as a strong thick stratum, covering the head and extending along the neck, trunk, and tail.

Intestinal diverticula are absent.

The ventral ganglion is large and thick; it is located at about the midlength of the trunk and ⅔ of the ganglion extends over the anterior part of the trunk while approximately ⅓ of the ganglion extends over the posterior part of the trunk, being closer to the neck than to the posterior septum. The ganglion does not occupy the total width of the trunk, and it is not as large as in *S. legazpichessi* and most other species of *Spadella.*

The pair of lateral fins extends from the region of the opening of the oviducts to the seminal vesicles. The fins are completely rayed. The caudal fin is long, spatula-shaped, rounded laterally and wider at the tip of the tail segment, and ends with a straight posterior edge. It is independent of the posterior end of the lateral fins. Its origin is anterior to the posterior end of the seminal vesicles. The portion of the tail segment surrounded by the tail fin is about ⅓ of the tail segment.

The adhesive digital organs, located ventrally at each side of the tail segment in the region of the seminal vesicles, are formed by 2 fingerlike processes, similar to the thumb and index fingers of a human hand, the thumb being broader at the base than the index finger. Both the thumb- and index-like fingers at each side are strengthened by muscle-like fibers. At the ventral part of the tip of each finger is an oval pad of very fine papillae. These adhesive digital structures develop from the ventrolateral sides of the posterior part of the tail segment, and are independent of the lateral and tail fins and seminal vesicles. These digital organs extend ventrally to support the animal far away from the substratum while it is resting or when it is crawling. These organs help to attach the animal to the substratum (Fig. 2D). The fins are used during darting and swimming activities. Both types of behavior, attachment to the substratum and crawling and swimming, have been directly observed in *Spadella* by the author.

The digital structures of young 1.75 mm specimens up to the fully mature 3.75 mm specimens were of the same shape, and had the same number of fingers and structural characteristics. Thus, there is no evidence that the number of digital formations increases with growth in *S. pimukatharos,* as reported by Feigenbaum (1976) for *S. schizoptera.* Probably an increase with growth in the number of fingers in these adhesive organs does not apply to every species of *Spadella.* Also, the increase in the number of fingers Feigenbaum (1976) observed for *S. schizoptera* was due to the material he analyzed, that is, his specimens ranged from larval stage (newborn) to 14-day-olds. It is obvious that in growth from larvae to the phase before Stage I of maturity, some

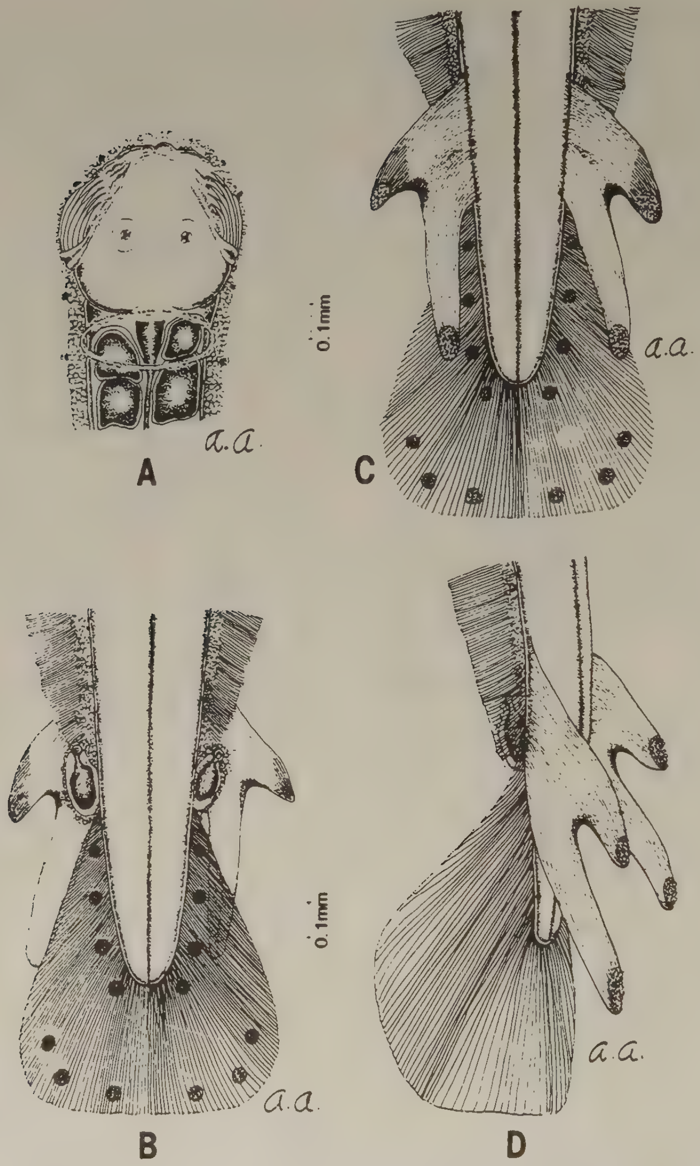

Fig. 2. *Spadella pimukatharos*: A, Dorsal view of head and neck; B, Dorsal view of posterior part of tail segment; C, Ventral view of posterior part of tail segment; D, Right side view of posterior part of tail segment showing dorsolateral position of seminal vesicles, and ventrolateral position of adhesive digital organs.

changes in meristic characteristics will be found, but does not imply that such changes take place during the development from Stage I to fully mature Stage IV.

From the ventral side to the dorsal side of the animal, the sequence of anatomical structures is: digital organs, tail fin, posterior part of lateral fins, seminal vesicles (Fig. 2D).

The ovaries extend to the neck region and fill the trunk cavity. The ova are large, hexahedral, with roundish edges and angles. They are pressed together and completely fill the ovaries, which compress the intestine towards the ventral side (Fig. 1A, B).

The oviducts open by cups dorsolaterally. The lateral fins extend ventrally anterior to the opening of the oviducts. The ventral position of the fins and dorsal setting of the oviducts results in an adequate functional device to ensure the transference of sperm during copulation (Fig. 1A).

The seminal vesicles touch both the posterior end of the lateral fins and the anterior end of the caudal fin. Seminal vesicles are protected ventrally by both the posterior and anterior parts of the lateral fins and tail fin. The seminal vesicles are oval, and smaller than in *S. legazpichessi*. The seminal vesicles resemble small amphores without handles, with anterior short neck open at the top of the neck. They are covered by the alveolar collarette tissue (Fig. 2B).

Sensory spots with sensory cilia are distributed over the tail fin and along the edge of the lateral fins and collarette from the head to the posterior part of the trunk. Fourteen of these spots occur on the tail fin, and about 10 appear to be distributed at each side from the head to the region of confluence of collarette and anterior part of lateral fins. More spots extend along the edges of the lateral fins.

Remarks.—*Spadella pimukatharos* differs from *S. schizoptera, S. nana,* and *S. legazpichessi* in the general aspect of the body, corona ciliata, hooks, ventral ganglion, shape of ova, shape of seminal vesicles, and shape of the adhesive organs. (See Table 1).

According to Conant (1895), *S. schizoptera* has two pairs of lateral fins, whereas *S. nana, S. legazpichessi,* and *S. pimukatharos* have one pair of lateral fins. Owre (1963: 380) indicates regarding *S. schizoptera,* "The specimen from Soldier Key has a single pair of lateral fins which begin 0.14 mm anterior to the transverse septum and terminate in the adhesive organs"). Owre (1972) referring to *S. schizoptera* explains it as "having 1 (2?) pairs of lateral fins," but unfortunately her illustration of this species does not elucidate this question, since the oviducts are drawn extending over the fins, making it impossible to define whether the lateral fins are one or two pairs. A ventral view of the species will show clearly the particular characteristics of the lateral fins. *Spadella schizoptera* has also been described by Conant (1895) as having intestinal diverticula, which are absent in the other species of *Spadella.*

Distribution.—The specimens of *Spadella pimukatharos* were collected by James (Tony) R. Chess at 10 m depth in 10 cm core samples (coffee cans) at Fisherman's Cove in Santa Catalina Island, California. According to Chess (pers. comm.), the highest number of specimens were obtained from locations where fragments of the coralline algae *Lithothamnion australe* made up more than 50% of the sediment, and at those locations the species occurred in densities of 3566/m^2, while in finer sediments the species was less abundant, from 127–636/m^2. Chess (pers. comm.) also indicated that the species was present in all five samples obtained from Fisherman's Cove on 13 Mar 1985.

Chess (pers. comm.) noted that specimens of this species were not found in samples from Fisherman's Cove obtained from 1972 to 1975, and during 1980, 1981, and 1983. However, specimens of *S. pimukatharos* were abundant at Fisherman's Cove during collections of 1984 and 1985.

Thus, it is not clear whether this species is established in this area. Either it is endemic in the region, or the population has been transported by the strong flow of warm waters from the south and has become established incidentally in Santa Catalina Island waters. It should be remembered that the warm climate in the Californian Pacific during 1984 and 1985 was probably related to the strong El Niño conditions of the South Pacific during 1982–1983, although the warmer than normal conditions persist in

Table 1.—Differential characteristics of species of *Spadella* having digital adhesive organs with apical papillar pads.

	Species			
Character.	*Spadella schizoptera* Conant, 1895	*Spadella nana* Owre, 1963	*Spadella legazpichessi* Alvariño, 1981	*Spadella pimukatharos* n. sp.
Body length mm	1.9–4.9, wider at level of posterior septum	0.75–2.70	1.8–2.2, trunk strong, opaque, widest at midlength	1.75–3.73, strong, opaque almost same width from head to tail
Head	Broader than body, narrow neck. 1 pair of pads at mouth	Broader than body. Neck distinct. 1 pair of papillae between anterior teeth and mouth	Large, wider than body. Neck clearly distinct	Roundish, same width as trunk. Neck slightly distinct. 1 pair of round pads in front of mouth
Tail segment as % of total length	47.0–53.7	40–50	50	50 or slightly more
Lateral paired fins	2 pairs. Anterior pair extending from level posterior to ventral ganglion to opening of oviducts. Second pair from this point to seminal vesicles. Only 1 pair of lateral fins (Owre 1963)	1 pair extending from a level anterior of oviducts to seminal vesicles	1 pair extending from level of oviducts to seminal vesicles	1 pair extending from level anterior of opening of oviducts to seminal vesicles
Caudal fin	Long, spatula-shaped	Spatula-shaped, starting at posterior end of seminal vesicles	Spatula-shaped, starting at posterior end of seminal vesicles. 12 sensorial spots. No rayless zone	Long, spatula-shaped, starting at level of posterior end of seminal vesicles. No rayless zone
Eyes			Large, oval, pigment in longitudinal band tilted to sides, and short band perpendicular at midlength	Large, round, pigment in longitudinal band crossed by short band pointing to center of head
Hooks	8–11, long curved, sharp pointed	5–9	8–9 at each side, thick, strongly curved	7–9 at each side, thin, curved
Anterior teeth	2–3, long, slender, curved towards midline	1–3, innermost longer than others, curved towards midline	Up to 5 on each side. First 3 longer than others. Third on each side longest. Curved towards ventral side	2–3 on each side, thin, short, pointed
Posterior teeth	None	None	None	None

Table 1.—Continued.

Character	Species			
	Spadella schizoptera Conant, 1895	*Spadella nana* Owre, 1963	*Spadella legazpichessi* Alvariño, 1981	*Spadella pimukatharos* n. sp.
Corona ciliata	Three-cornered or pear-shaped. Part on head and neck	Variable in shape, extending from neck towards head	Ring-shaped at dorsal part of neck	Elliptical at dorsal side of neck. Transverse axis more than twice length of vertical axis
Ventral ganglion	Large, thick, overlaid by numerous sensory spots	As broad as long	Large, thick, at midlength of trunk. About 50% length of trunk, as close to neck as to posterior septum	Large, thick, at midlength of trunk, extending ⅔ to anterior part and ⅓ to posterior part. Closer to neck than to posterior septum. Not covering ventral width
Sensorial spots	Abundant, distributed in longitudinal and transverse rows	Symmetrically arranged in pairs on caudal fin, and longitudinal rows on body	Symmetrically arranged on tail fin (6 on each side). Conspicuous along edge of lateral fins, 6 or more on each lateral edge of collarette	Symmetrically arranged 14 on tail fin, other 10 on each side from head to confluence of collarette with lateral fins. More along edges of lateral fins
Ovaries	Reaching neck or anterior end or midlength of ventral ganglion	Reaching to neck. 2–5 huge ova, pressing intestine into "S" shape	Reaching neck region. Few large ova, pushing intestine into sinuous shape	Reaching neck region. Ova large, hexahedral, packed together, filling ovaries, pressing intestine towards ventral side
Seminal vesicles	Ellipsoidal, reniform, touching both lateral and tail fins	Oval, roundish, anterior to tail fin. Protected ventrally by lateral and tail fins	Ellipsoidal, reniform, touching posterior end of lateral fins and anterior end of tail fin. Open at middle edge towards posterior half of vesicle	Small, oval, amphora- or flask-shaped, anterior thin neck opening dorsally at anterior end
Intestinal diverticula	Present or absent according to various authors	Absent	Absent	Absent
Adhesive digital organs	Hand-shaped, continuation of lateral fins, with 4, 5, 6 fingerlike processes with adhesive papillae	Ventrally from posterior end of lateral fins to seminal vesicles. Divided into 2 stout fingers with muscular fibers	3 long, thin fingers on each organ, not connected to fins, but attached to tail at level of seminal vesicles. Outermost finger	2 fingers on each side, like thumb and index of human hand, strengthened by muscular fibers, with oval pad of

Table 1.—Continued.

	Species			
Character.	*Spadella schizoptera* Conant, 1895	*Spadella nana* Owre, 1963	*Spadella legazpichessi* Alvariño, 1981	*Spadella pimukatharos* n. sp.
		and papillae or tubercules at tip. First finger longest	longest. Strengthened by thin muscular fibers. Large sensorial club at ventral side of tail	papillae at ventral tip
Collarette	Thick at neck, extending to seminal vesicles	Thick at neck, tapering towards seminal vesicles	Thick at neck, extending along body, tapering at posterior part of tail segment	Strong, covering head and body
Geographic distribution	Bahamas, Florida. Records from Japan (Yosii and Tokioka 1939), and from New South Wales, Australia (Mawson 1944) may be erroneous	Florida	Enewetak (Marshall Islands)	Fisherman's Cove, Santa Catalina Island, California

California up to this date. It is well known from the literature that during El Niño conditions, several populations from tropical eastern Pacific waters have been transported north off the U.S. and Canada, reaching as far north as Alaska. There is no information on the species of *Spadella* inhabiting waters south of San Diego, California. Thus, the question of whether *S. pimukatharos* is endemic to Santa Catalina Island or is transported to this area from a southern source will be elucidated when the populations of *Spadella* inhabiting Mexican and Central American Pacific waters are studied.

Etymology.—The specific name is a combination of "Pimu" and "katharos." Pimu was the original name of Santa Catalina Island until 1542, and *katharos* is the Greek root for Catalina, which means pure, clean, unsullied. This island was discovered in 1542 during the Spanish Expedition under Juan Rodríguez Cabrillo with two vessels, the *San Salvador* and the *Victoria*. He named San Salvador and Victoria the islands now called San Clemente and Santa Catalina (Instituto Historico de Marina 1943). In 1602, during the Spanish Expedition of Sebastián Vizcaino with three vessels, *San Diego, Santo Tomás* and *Tres Reyes Magos,* the islands were named San Clemente and Santa Catalina (Instituto Histórico de Marina 1944). The original name of San Clemente was Limun (Instituto Histórico de Marina 1943). Both Rodríguez Cabrillo and Vizcaíno indicate in their diaries of navigation that Santa Catalina, San Clemente, and the Channel Islands were inhabited by native Indians of California. Pimu, Pimuna, Pimun-gen apparently also meant "People of the Sea," and the Spaniards used to call these indians Pipimar and Pipimares (Kroeber 1925). According to Rodríguez Cabrillo and Sebastián Vizcaíno, the indigens fed mainly on fish, and sardines were very abundant.

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ASSESSING NORTHERN ELEPHANT SEAL FEEDING HABITS BY STOMACH LAVAGE

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Abstract

Stomach lavaging was used to study the feeding habits of northern elephant seals (*Mirounga angustirostris*) found on San Miguel Island, California, during the spring of 1984. Fifty-nine elephant seals were chemically immobilized with an intramuscular injection of ketamine hydrochloride. Once immobilized, an animal's stomach was intubated, filled with 3–4 liters of water to create a slurry of the undigested food items, and evacuated into a collection device. The stomachs of 57 (96.6%) of the animals lavaged contained identifiable parts of prey. Twenty-nine different food items were identified, 12 of which have not been previously reported as prey of the northern elephant seal: two teleost fish, *Coryphaenoides acrolepis* (Pacific rattail) and another unidentified macrourid; two crustaceans, *Pasiphaea pacifica* (glass shrimp) and *Euphausia* sp.; six squid, *Abraliopsis felis*, *Gonatus berryi*, *Histioteuthis dofleini*, *Cranchia scabra*, *Taonius pavo*, and *Galiteuthis* sp. and two octopi, *Octopus dofleini* and *Octopus rubescens*.

The following prey species were found in at least 20% of stomachs lavaged: *Octopoteuthis deletron* (squid), *Merluccius productus* (Pacific whiting), *Gonatopsis borealis* (squid), *Pleuroncodes planipes* (pelagic red crab), *H. dofleini* and *H. heteropsis*. The diversity of habitats in which many of these prey are commonly found indicates that the northern elephant seals from San Miguel Island are capable of foraging in a variety of marine environments (epipelagic, mesopelagic, bathypelagic, neritic and benthic) and may only be limited by the depth to which they can dive.

Key words: Northern elephant seals, feeding habits, stomach lavage, ketamine immobilization.

Northern elephant seals have been the subject of numerous behavioral and population studies over the last three decades (*e.g.*, Bartholomew 1952, Le Boeuf 1974, Antonelis *et al.* 1981, Reiter *et al.* 1981, Cooper and Stewart 1983); yet relatively little is known about their feeding habits. Our knowledge of this species' diet has been principally based on the stomach contents of animals found dead or stranded along the coasts of California and Oregon (Huey 1930, Freiberg and Dumas 1954, Cowan and Guiguet 1956, Morejohn and Baltz 1970, Antonelis and Fiscus 1980, Jones 1981, Condit and Le Boeuf 1984, Huber *et al.* 1985, Hacker 1986). In many instances it is apparent that the health of these animals had been compromised prior to their death or discovery on shore. Consequently, current information on the feeding habits of northern elephant seals may not reflect the typical diet of healthy individuals capable of normal foraging behavior.

Several methods of obtaining dietary information from pinnipeds increase the probability of collecting data from healthy animals. Killing healthy animals to examine the contents of their stomachs is one method. This may not be desirable, however, if the individual animal of interest is part of a long-term behavioral study or if the species studied is threatened or endangered. Alternatively, non-lethal methods of collecting identifiable remains of prey species include the analyses of scats and spewings (Bailey and Ainley 1982, Brown and Mate 1983, North *et al.* 1983, Antonelis *et al.* 1984) and stomach lavaging (Hall 1977). Direct observation is also a technique which has been successful in unique circumstances where the animals forage in relatively shallow water and observations are made from land (*e.g.*, Jameson and Kenyon 1977, Bowlby 1981). Thus, a variety of methods are available for examining the feeding habits of healthy pinnipeds.

Here we detail a stomach lavaging technique used to assess the diet of northern elephant seals, and present the information on prey species obtained during our study. The undigested parts of food items (principally crustacean parts, cephalopod beaks and fish otoliths) recovered from the stomachs were used to identify the prey of the northern elephant seal. Possible differences between the diets of subadult males and adult females were examined, and comparisons were made between the use of stomach lavage and scat analysis for the assessment of dietary information. We also evaluated the use of ketamine hydrochloride for immobilizing northern elephant seals during the lavaging procedure.

MATERIALS AND METHODS

This study was conducted on San Miguel Island, California, from 17 April through 3 May 1984. All of the animals lavaged were hauled out for spring molt on the sandy beaches at the west end of the island.

Assuming that elephant seals do not show obvious signs of molt until after they arrive on land, those showing the least amount of hair loss were presumed to be on land the least amount of time. Thus, we increased the probability of lavaging food parts from the stomachs of elephant seals by selecting those animals showing little or no sign of molt.

We captured each seal in a head bag (Stirling 1966) which measured 122 cm long, 70 cm in diameter at the opening and tapered to a diameter of 48 cm at the closed end. The bag was made of neoprene reinforced canvas with grommeted ventilation holes in the closed end. Ropes attached to four metal rings spaced equidistantly around the opening were used to hold the mouth of the bag open as it was placed over the animal's head and then pulled over the anterior portion of the animal's body.

After physically restraining each animal in the bag, we determined the sex and standard length in order to estimate the animal's weight using regression equations of length to weight. Standard length measurements ranged from 210–274 cm for females and from 203–300 cm for subadult males. Although we used the regression equations of the length to weight relationships reported for southern elephant seals (*Mirounga leonina*) by Ling and Bryden (1981), we assumed those weight estimates would be consistently more accurate than our subjective estimates. Weight estimates were used to calculate the dose of ketamine hydrochloride (hereafter referred to as ketamine) used for immobilization. All ketamine doses were injected intramuscularly in the pelvic area using a 20 cc syringe and a spinal needle (8.9 cm × 18 gauge). The capture bag was removed from the seal's head as soon as a decrease in muscle control was observed. If no evidence of immobilization was observed after 10 to 15 min the animal received an additional injection with half of the original dose of ketamine. A maximum of two additional half doses was used.

After immobilizing the seal a clear tube of flexible PVC (2.54 cm inside diameter, 0.48 cm wall thickness, 3 m length) was inserted into the stomach. Rounding the edges of the end of the tube and coating it with surgical lubricant facilitated passage of the tube into the stomach. To increase the chance of retrieving parts of prey species, a rectangular port (1.5 × 4.0 cm) was cut in the side of the tube about 1.5 cm from the end (Fig. 1). In most cases the lavage tube was passed through a 3.8 cm hole in a block of wood (60.0 cm × 3.8 cm × 7.6 cm) which was placed in the animal's mouth to prevent the seal from biting and collapsing the tube. Once in place, the lavage tube was connected to the discharge fitting of a manually operated suction pump and approximately 3 to 4 liters of sea water were pumped into the animals's stomach (Fig. 1a). The suction fitting of the pump was then connected to one of two hose fittings on an airtight 10 liter collecting bottle while the other fitting was attached to the lavage tube (Fig. 1b). A vacuum was created in the collecting bottle and the slurry of water and undigested food parts were suctioned from the stomach

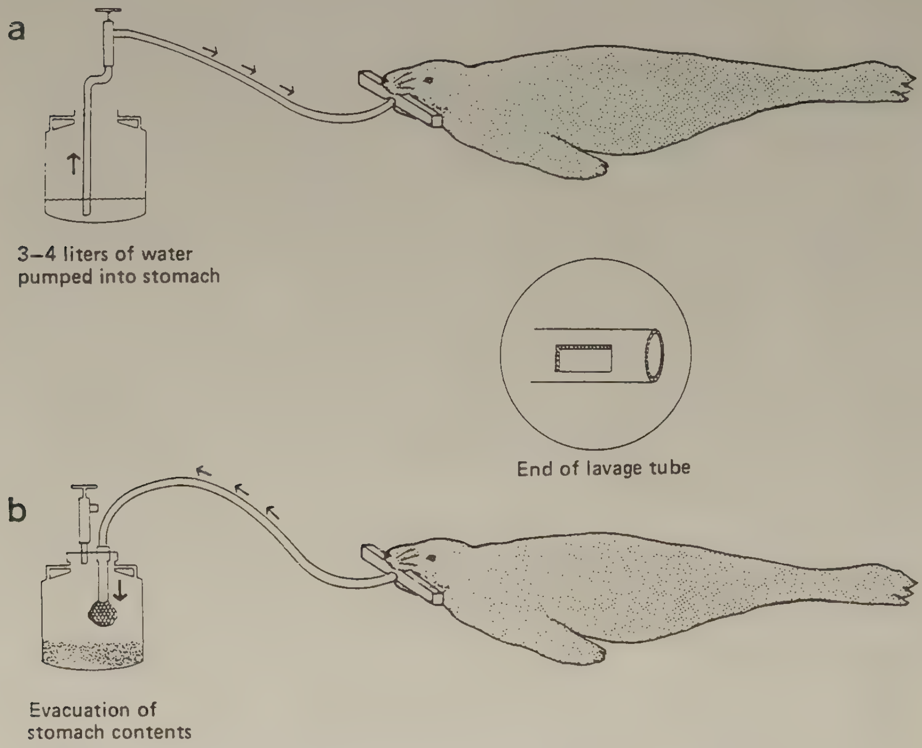

Figure 1. Illustration of the lavage apparatus used to (a) fill the seal's stomach with 3–4 liters of water and (b) evacuate the stomach contents.

into the bottle. An intermediate screen with a mesh size of approximately one mm was attached to the intake tube of the collecting bottle to separate the undigested food items from the liquid. The lavage tube was removed and rinsed with water immediately after the lavaging procedure. Any food items remaining inside the tube were rinsed into the sample. Finally, the remaining liquid in the collecting bottle was passed through a second screen (0.5 mm mesh) to insure that all identifiable parts of prey had been recovered.

To test the reliability of the lavaging procedure, we conducted a second stomach lavage on seven elephant seals immediately after the first lavage and then compared the frequency of occurrence of prey items in the two lavages. We also compared the success of obtaining feeding habit information from the lavaged seals with that from scat analysis. On 5 May 1985, 29 northern elephant seal scats were collected on the west end of San Miguel Island, California.

Two of the authors (G. Antonelis and M. Lowry) determined the prey species of teleost fish lavaged from the stomachs of the northern elephant seals by identification of sagital otoliths. Cephalopod beaks recovered from the stomach of the northern elephant seals were identified by another of the authors (C. Fiscus), and F. Hochberg (Santa Barbara Museum of Natural History, Santa Barbara, CA) identified the crustaceans and the tunicates.

Table 1. Occurrence of apnea in northern elephant seals immobilized with ketamine according to the dose rate (mg/kg) and sex and size range of the animals studied.

Sex of animal and dose rate of ketamine (mg/kg)	Single injection (n = 45)				Multiple injections (n = 14)[a]			
	Without apnea		With apnea		Without apnea		With apnea	
	No.	Percent of total	No.	Percent of total	No.	Percent of total	No.	Percent of total
Females[b] and males[c]								
2.01–2.50 (n = 2)	—	—	—	—	2	100	—	—
2.51–3.00 (n = 9)	6	67	2	22	1	11	—	—
3.01–3.50 (n = 19)	10	53	2	11	5	26	2	10
3.51–4.00 (n = 11)	5	45	5	45	1	10	—	—
4.01–4.50	—	—	—	—	—	—	—	—
4.51–5.0 (n = 2)	2	100	—	—	—	—	—	—
Males[d]								
2.01–2.50 (n = 10)	4	40	3	30	3	30	—	—
2.51–3.00 (n = 5)	5	100	—	—	—	—	—	—
3.01–3.50 (n = 1)	1	100	—	—	—	—	—	—

[a] Animals receiving a second or third injection of half the original dose rate if no evidence of immobilization was achieved after 10–15 min.

[b] 210–283 cm standard length (std. ln.).

[c] 203–249 cm std. ln.

[d] 250–300 cm std. ln.

The age composition of the Pacific whiting (*Merluccius productus*) consumed by the elephant seals examined in this study was determined from the sizes of otoliths recovered from stomachs. Because of the rapid growth of *M. productus*, otolith differences in year classes are conspicuous and easily recognized during the first 3 yr of life (*see* fig. 12, Dark 1975). After 3 yr the growth rate slows, making detection of year classes much more difficult. Due to the amount of digestive damage to these otoliths their ages could only be estimated by visually comparing them to voucher otoliths from known age fish and classifying them into age categories according to their relative size and shape. We categorized *M. productus* into five age class categories: <1, 1, 2, 3 and 4–6 yr of age.

RESULTS

Immobilization with Ketamine

We immobilized 59 northern elephant seals with ketamine during this study. The responses of seals receiving various dose rates are shown in Table 1. Attempting to keep dosage levels to a minimum, we found that optimal dose rates for immobilization ranged from 2.51 to 3.50 mg/kg for males less than 250 cm in length and for all females (210 cm to 283 cm in length). The optimum dose for males greater than 250 cm was between 2.51 and 3.00

mg/kg. Forty-five seals were immobilized after the first injection, while 12 seals required a second injection and 2 required a third injection.

Apnea was observed in 23.7% of all seals injected. In those seals requiring additional doses apnea occurred only twice. Those seals exhibiting apnea remained immobile for an average of 81.6 min (n = 14, SD = 29.9 min), while those without apnea were immobile for an average of 12.1 min (n = 45, SD = 8.2 min). Muscle tremors were frequently observed during periods of apnea just prior to resumption of breathing.

One 4-yr-old male (length = 268 cm) died after being injected with a single 2.5 mg/kg dose of ketamine. Although a necropsy revealed no conspicuous abnormalities, a histological examination revealed some inflammatory cell infiltrates in the lung tissue.

Feeding Habits

The frequency of occurrence of the prey obtained from the stomachs of 59 northern elephant seals (25 subadult males and 34 adult females) by lavage are listed in Table 2. From this table it is apparent that cephalopods comprise the largest number of different prey species (n = 20) identified in this study. From this group *Octopoteuthis deletron* occurred most frequently (59.6%). Eight of the cephalopods that we identified (*Abraliopsis felis, Gonatus berryi, Histioteuthis dofleini, Cranchia scabra, Taonius pavo, Galiteuthis* sp., *Octopus dofleini, Octopus rubescens*) have not been previously reported as prey of the northern elephant seal. Forty-five (78.9%) stomachs contained either identifiable or unidentifiable parts of cephalopods.

Of the prey listed in Table 2 the crustacean *Pleuroncodes planipes* was the most frequently occurring (77.2%) prey species identified during this study. The two other crustaceans identified during this study (*Pasiphaea pacifica* and *Euphausia* sp.) have not been reported previously as prey of the northern elephant seal.

The identifiable parts from three groups of fishes (teleosts, elasmobranchs and cyclostomes) were obtained from lavaged stomachs (Table 2). *Merluccius productus, Sebastes* spp. and two macrourid species (*Caryphaenoides acrolopis* and an unidentified species) were identified from otoliths. Egg cases of two elasmobranchs (*Cephaloscyllium ventriosum* (Pacific rattail) and an unidentified species) and one cyclostome (*Polistotrema stouti*) were identified. The cyclostome, *Lampetra tridentata*, was identified on the basis of its characteristic mouth parts. The two macrourids have not been previously reported as part of the northern elephant seal's diet. Forty-five (75.7%) stomachs contained either identifiable or unidentifiable parts of fish.

Merluccius productus was the most frequently occurring prey species of fish (29.8%); 154 otoliths from this species were lavaged from the stomachs of the elephant seals in this study. Figure 2 illustrates the estimated age composition of all *M. productus* otoliths recovered from the stomachs of elephant seals in this study. Eighteen percent (n = 27) of the otoliths were classified as juveniles, less than 1 yr of age, and 19% (n = 29) of the sample consisted of 1-yr-

Table 2. Frequency of occurrence and habitat of prey lavaged from the stomachs of 59 northern elephant seals.

Prey species	Frequency of occurrence: Number of stomachs	Frequency of occurrence: Percent of stomachs	Marine environmental zone[b]
Cephalopods			
Octopoteuthis deletron[a]	34	59.6	Ba-M-E
Histioteuthis dofleini	18	31.6	Be-M-E
Histioteuthis heteropsis	16	28.1	Be-M-E
Gonatopsis borealis	13	22.8	M-E
Galiteuthis sp.[a]	11	19.3	M-E
Onychoteuthis borealijaponicus	10	17.5	E
Gonatus berryi[a]	10	17.5	M-E
Gonatus sp. (type 2)	10	17.5	M-E
Chiroteuthis calyx	7	12.2	M-E
Vampyroteuthis infernalis	5	8.8	Be-M
Chiroteuthidae	4	7.0	M-E
Taonius pavo[a]	4	7.0	Ba-M
Gonatus sp.	4	7.0	M-E
Ocythoe tuberculata	3	5.3	M-E
Abraliopsis felis[a]	2	3.5	M-E
Moroteuthis robusta	2	3.5	Be
Cranchiidae	2	3.5	E
Octopus rubescens[a]	2	3.5	Be
Cranchia scabra[a]	1	1.8	E
Octopus dofleini[a]	1	1.8	Be
Crustaceans			
Pleuroncodes planipes	44	77.2	E
Pasiphaea pacifica[a]	8	14.0	E
Euphausia sp.[a]	4	7.0	E
Teleosts			
Merluccius productus	17	29.8	N
Sebastes sp.	5	8.8	N-Be
Coryphaenoides acrolepis[a]	2	3.5	M
Macrourid (not *C. acrolepis*)[a]	1	1.8	M
Elasmobranchs			
Cephaloscyllium ventriosum (egg case)	4	7.0	Be
Elasmobranch (egg case)	1	1.8	Be
Cyclostomes			
Lampetra tridentata	4	7.0	A
Polistotrema stouti (egg case)	1	1.8	Be
Tunicate			
Pyrosoma atlanticum	10	17.5	M-E

[a] Not previously reported as prey of the northern elephant seal.

[b] E = epipelagic, M = mesopelagic, Ba = bathypelagic, Be = benthic, N = neritic, A = anadromous.

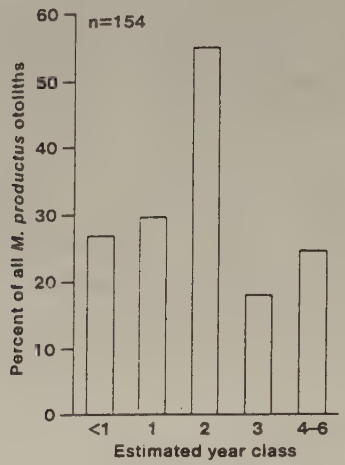

Figure 2. Estimated age of *Merluccius productus* (Pacific whiting) otoliths lavaged from the stomachs of northern elephant seals.

olds. The 2-year-old age class occurred most frequently (36%, *n* = 55), while 3-year-olds represented only 11% (*n* = 18) of the *M. productus* otoliths. The combined occurrence of the 4- to 6-year-olds was 16% (*n* = 25).

The tunicate *Pyrosoma atlanticum* was recovered from 18% (*n* = 10) of the elephant seal stomachs lavaged during this study.

Table 2 also lists the marine environmental zones where these various prey occur (Schmitt 1921, Thompson 1948, Cox 1963, Miller and Lea 1972, Roper and Young 1975, Butler 1980). Most prey (*n* = 24) occur in portions of the pelagic zone (epipelagic, mesopelagic, bathypelagic) while a few (*n* = 11) are found in the benthic or neritic zones. One prey item is anadromous.

For the seven seals that were lavaged twice, remains of 15 different prey were recovered during the first lavage, while evidence of only 7 prey was recovered from the second lavage. All of the prey species recovered from the second lavage were also present from the first lavage. Additionally, a necropsy of the subadult male (No. A66) that died during our study revealed that with the exception of two shark egg cases, which were too large to fit in the lavage tube, the same food items recovered from the lavage were also in the stomach.

Only 6 (21%) of the 29 scats collected contained identifiable parts from four prey species (*O. rubescens*, *Chiroteuthis calyx*, *Pleuroncodes planipes* and *M. productus*). In comparison, the recovery of identifiable prey species from the stomach lavaging technique (Table 2) was more productive, since it yielded dietary information from 57 out of 59 (97%) of the northern elephant seals examined. All of the prey found in the scats were also recovered from the stomachs of the lavaged seals.

The diets of 25 subadult male and 34 adult female northern elephant seals were compared according to the frequency occurrence of all prey identified in the six major prey categories: cephalopods, crustaceans, teleosts, elasmobranchs,

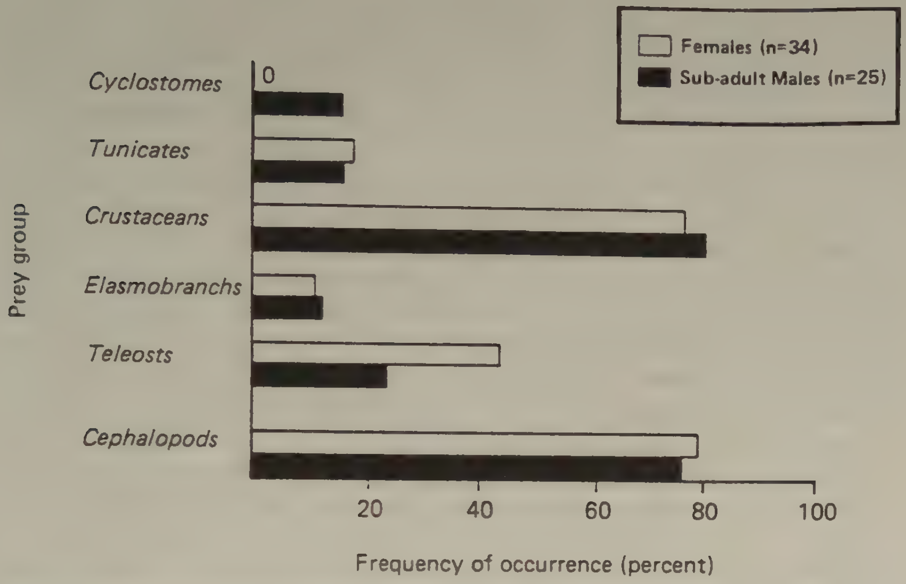

Figure 3. Frequency of occurrence of the six major prey categories lavaged from the stomachs of sub-adult male and female northern elephant seals.

cyclostomes and tunicates (Fig. 3). There was no significant difference between the two sexes (Chi-square test, $\alpha = .05$).

DISCUSSION

The use of ketamine has been demonstrated to be a relatively safe drug for immobilizing northern elephant seals in both this study and in the study by Briggs *et al.* (1975). Slight muscle tremors have been reported as a common side effect of ketamine (Geraci 1973) and observed in both our study and in the study by Briggs *et al.* (1975). In our study, however, conspicuous muscle tremors were usually associated with apnea, a condition not reported by Briggs *et al.* (1975). Apnea occurred in 14 of 59 seals in our study. Increased lacrimation and salivation were also commonly observed in our study but were not reported by Briggs *et al.* (1975). Perhaps these differences are related to seasonal differences in the physiological condition of the seals during the late spring (this study) and late winter (Briggs *et al.* 1975). Differences may also be due to the use of the head bag for the capture of animals before they were injected with ketamine during our study. This method was not used by Briggs *et al.* (1975) as they did not restrain the animals before they were injected.

For future work with northern elephant seals, several other drugs may be used in conjunction with ketamine to reduce some of these undesirable side effects. Xylazine has been used in combination with ketamine to facilitate immobilization and inhibit muscle tremors, but its success at immobilizing animals without inhibiting respiration has been varied when used on Galapagos fur seals, *Arctocephalus galopagoensis*. Galapagos sea lions, *Zalophus californianus wollebaeki* (Trillmich and Wiesner 1979, Trillmich 1983) and gray seals, *Halichoerus grypus* (Parry *et al.* 1981, Baker and Gatesman 1985). Furthermore, Geraci *et al.* (1981) have used diazepam to reduce the side effects of ketamine on several species of phocid seals (gray seals, harbor seals, *Phoca vitulina,* harp seals, *Phoca groenlandicus* and ringed seals, *Phoca hispida*). Atropine can be used to reduce excessive lacrimation, salivation and mucus production (Geraci 1973, Baker and Gatesman 1985). This becomes especially important when attempting to minimize the accumulation of fluid in the lungs, a condition which could have been a complicating factor in the death of the animal in this study. Finally, doxapram hydrochloride has been used as a respiratory stimulant on gray seals (Parry *et al.* 1981) and should be considered during future work on northern elephant seals when apnea occurs.

Despite our attempts to standardize the dose rate of ketamine by estimating animal weight on the basis of standard length, and the use of syringe and needle to insure an accurate placement of the intramuscular injection, variation in animal response was observed. Similar dosages which had no effect on some animals were enough to completely immobilize or cause apnea in others. Possible explanations for this variability include: error in the estimation of animal weight, differences between sexes, variability in the degree of vascularization of a seal's muscle tissue around the site of injection or differences in the physiological condition of individual animals at the time of injection. Similar variation in animal response to comparable dosages of ketamine has also been observed in other field studies of phocids (Geraci 1973, Briggs *et al.* 1975, Engelhardt 1977). Fortunately, despite this variability in response, ketamine has a relatively wide margin of safety when used on phocids. Its use on some otariids, however, appears to inhibit breathing more frequently (Trillmich 1983, DeMaster and Antonelis unpublished observations) and may not be recommended if other alternative methods of immobilization are available.

It is apparent from this study that northern elephant seals that haul out at San Miguel Island, California, forage on a variety of prey species that range from squids, crustaceans and tunicates in several pelagic zones, to octopi, teleosts, elasmobranchs and cyclostomes occurring in the neritic and benthic areas of the sea. This indicates that northern elephant seals forage in a variety of marine environments and may be limited only by the depth to which they can dive. Our information from stomach lavage corroborates previous interpretations of this species' basic foraging habits which have been based primarily on the opportunistic examination of dead animals.

Of the 12 newly identified prey of the northern elephant seal 8 are cephalopods. *Octopoteuthis deletron* was the most frequently occurring cephalopod (59.6%) in our study and in that of Condit and Le Boeuf (1984). Other squid occurring in more than 10% of the stomachs examined in our study included: *Gonatus berryi*. *Gonatus* sp. (type 2), *Gonatopsis borealis*. *Histioteuthis dofleini*. *Histiotheuthis heteropsis*. *Chiroteuthis calyx* and *Galiteuthis* sp. These results may reflect the importance of squid in the diet, but interpretations should be made with caution since cephalopod beaks may resist digestion and result in an over-representation of squid and an under-representation of fish otoliths (*e.g.*, Miller 1978, Pitcher 1980). Further, if the frequency of occurrence of the identifiable and unidentifiable parts of cephalopods and fish are compared, the importance of the two groups appears to be much more similar with values of 78.9% and 75.4%, respectively.

The pelagic red crab (*Pleuroncodes planipes*) was also a frequently occurring prey of the northern elephant seals in this study. Although it has been reported as a prey of northern elephant seals in a recent report (Hacker 1986), its presence in 77.2% of the stomachs indicates it may be an important food item when available. Boyd (1967) found that pelagic red crab are normally found on the continental shelf of southern Baja California, Mexico, and are occasionally transported northward by the Davidson and California countercurrents into the waters off the California coast in January and February. During abnormal years, such as the 1983 El Niño Southern Oscillation (ENSO) event, these currents are intensified and persist for longer periods. This phenomenon results in the northward transport of large numbers of pelagic red crabs into northern latitudes. The occurrence of this prey in the diet of the northern elephant seal is apparently related to their availability at the San Miguel Island area during the 1983 ENSO. Given the high frequency of occurrence for this prey item, however, we would expect to identify the pelagic red crab as a common prey of the northern elephant seal at haul-out sites in Baja California.

Pacific whiting (*Merluccius productus*) was the most frequently occurring teleost prey of the northern elephant seal. California sea lions also prey on Pacific whiting in the waters near San Miguel Island (Antonelis *et al.* 1984). Apparently, both the elephant seal and the sea lion forage mostly on 1- and 2-year-old fish. This is consistent with out knowledge of the distribution of Pacific whiting: younger age classes are more abundant in the southern portion of their range especially during the spring when most of the older age classes move north of Point Conception (Bailey *et al.* 1982). When we compared the feeding habits of the subadult males and adult females, we were not surprised to find that the two groups do not differ significantly since individuals from both groups were presumably lavaged soon after they had returned to the island from feeding at sea during approximately the same time period. Both groups appear to exploit similar resources when foraging in the waters around San Miguel Island. Intraspecific differences are probably more likely to occur spatially and temporally as various age and sex classes migrate into different locations at sea (Condit and Le Boeuf 1984) or as seasonal changes in the availability of various prey items occur.

Results from the seven seals lavaged twice indicate that a relatively small proportion of identifiable prey items remain in the stomach after the first lavage and that a single lavage was sufficient to recover a representative sample of the prey items in the stomach. This is important when considering the prudence of subjecting an animal to a second lavage and to the effects of a possible additional injection of ketamine to maintain immobilization. Therefore, the well-being of the seal must be considered against the amount of added information that might be obtained when conducting multiple stomach lavages on a single animal. We believe that when the number of seals examined is large (*e.g.*, this study), a single stomach lavage per chemically immobilized seal is the preferred method of obtaining dietary information. However, when the number of seals examined is small or when the feeding habits of specific individuals are of interest, multiple stomach lavages may be necessary to maximize the amount of dietary information recovered from each individual.

Clearly additional information is needed to obtain a better understanding of this species' feeding habits which may change on a seasonal or annual basis. Possible differences between various age class and sex categories need to be examined for a better understanding of the species' foraging ecology. Feeding studies of captive animals are also necessary for a better understanding of prey digestion rates and the passage of hard parts of prey through the gastrointestinal tract, thus allowing us to more accurately interpret the results of stomach lavage studies on seals in the wild.

The stomach lavage technique described in this study does have some limitations. The size of the prey items recovered is limited to the inside diameter of the tube. This tends to bias the sample for small, digested prey and against large, undigested prey. There could also be a bias for prey with hard parts that tend to resist digestion and remain in the stomach for longer period of time. Furthermore, the possible occurrence of hard parts of secondary prey (*i.e.*, from the stomach of the prey) could bias the results of stomach content analysis (Perrin *et al.* 1973).

The results of this study have shown that a collection of scats from northern elephant seals for food habit information is not as productive as the stomach lavage. This observation is corroborated by numerous other unsuccessful attempts by one of the authors (Antonelis) and B. Stewart (personal communication, Hubbs Marine Research Center, San Diego, California) to describe the diet of the northern elephant seal through scat analysis. Clearly the most productive non-lethal method of collecting dietary information from healthy individuals of this species is through stomach lavage. We have also lavaged the stomachs of physically restrained northern fur seals, *Callorhinus ursinus* and California sea lions, *Zalophus californianus californianus*, with comparable success (unpublished observations). However, for these species scat analysis has proven to be a more productive method of determining the diet. Therefore, the preferred non-lethal method for obtaining feeding habit information may differ with each pinniped species. A distinct advantage in using the stomach lavage technique is the ability to select sample size, time, location, age and sex of the individual animals to be studied.

By modifying the stomach lavage techniques described by Hall (1977) and utilizing ketamine for chemical immobilization, we have obtained new information on the diet of the northern elephant seal. The diversity of its prey indicates that the northern elephant seal may be a true generalist in its foraging behavior, a factor which has probably enhanced its ability to recover from near extinction in the early 1900s.

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Assistance during the examination of several different cephalopod beaks from our collection by F. G. Hochberg resulted in the identification of *Gonatus berryi* and confirmation of the identity of several other species.

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8704

Seabird-Tuna Relationships

Like fishermen, fishery scientists can learn much about tuna by studying seabirds. Since 1976 biologists of the Pelagic Division, Southwest Fisheries Center, National Marine Fisheries Service, have been recording seabird observations in the eastern and central tropical Pacific. This work, begun on the 1976-1980 dolphin surveys, implicitly recognizes the biological entity of seabird-tuna-dolphin associations.

The studies have revealed a large-scale dichotomy in the apex, pelagic community that appears to involve feeding tactics: multispecies flocks that feed with yellowfin tuna, mainly in tropical waters north of the equator, are apparently sharply separated from virtually single-species flocks that occur largely south of the equator and that feed with skipjack or other small tunas. Boobies (*Sula* spp.) are the most abundant of the birds in the multispecies flocks, and, like most other species in the flocks, are facultative commensals with the tuna they follow. Overall, about 50% of these tuna schools were found to be with dolphins, primarily the spotted dolphin (*Stenella attenuata*) but also to a lesser extent spinner and common dolphins (*S. longirostris* and *Delphinus delphis*). Most other cetaceans in the eastern Pacific (some 20 kinds) were found to seldom associate with either tuna or birds. In the single-species flocks to the south, the sooty tern (*Sterna fuscata*), essentially an obligate commensal on tuna, predominates. Those flocks, and associated tuna, are seldom with dolphins. This dichotomy in community organization is a conspicuous biological feature of the eastern tropical Pacific, and indicates the existence of different, large-scale feeding regimes.

One implication from these species relationships is that ecologically successful species of sparsely productive, tropical seas will be those species capable of following or feeding with tunas—which by their annual fishery yields are evidently very successful in that habitat. Boobies, especially the red-footed and masked species (*S. sula* and *dactylatra*) are the most abundant of birds in tropical waters north of the equator, and are characteristic of flocks that feed with yellowfin tuna. The spotted dolphin is the most abundant cetacean in the eastern Pacific, and it too is closely associated with yellowfin. Sooty terns are the most abundant bird species south of the equator (and also in the central Pacific), and have a strong, commensal feeding relationship with skipjack or other small tunas there.

Differences in availability of tunas appear related to differences in productivity, and how tunas accordingly feed, as indicated by bird behavior. South of the equator, food is not apparently in large patches; the tuna there are fast moving, and their feeding bouts are brief. Only sooty terns seem to be very successful in following these tuna. In contrast, tuna on the purse seine grounds north of the equator feed on relatively long-lasting aggregations of surface prey, in association with several other, similarly feeding species of seabirds and dolphins. And where both "schoolfish" and longline tuna fishing are important (and "porpoise fishing" is not), as in some areas west of Panama and Costa Rica, the bird-tuna association is very variable, suggesting that the tuna there feed variously between surface and subsurface layers (presumably, birds do not build up flocks over schools not feeding long at the surface). Finally, the summer immigration of southern hemisphere Juan Fernandez and white-necked petrels (*Pterodroma externa* subspp.) onto the extensive yellowfin fishing grounds west of Clipperton Island indicates a reliable seasonal increase of production—and of surface-feeding tuna over which these birds flock. This is also indicated by the seasonal increase of fishing effort and catches there. The feeding of these petrels with tuna was not expected, as they are of a family of birds that are typically surface gleaners.

Future research will include analyses of areal changes in flock species diversity, in the degree to which flocks associate with tunas (as an indicator of tuna behavior and availability), studies of seasonal movements of flocks and flock behavior, and of the relationship of flock size to tuna-school tonnage.

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Monthly Variability in the Ocean Habitat off Peru as Deduced from Maritime Observations, 1953 to 1984

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BAKUN, A. 1987. Monthly variability in the ocean habitat off Peru as deduced from maritime observations,1953 to 1984, p. 46-74. *In* D. Pauly and I. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

Monthly time series, generated from summaries of maritime reports from the region off Peru, are presented for the period 1953 to 1984. These include sea surface temperature, cloud cover, atmospheric pressure, "wind-cubed" index of rate of addition of turbulent mixing energy to the ocean by the wind, wind stress components, solar radiation, long-wave back radiation, evaporative heat loss and net atmosphere-ocean heat exchange. All series are found to undergo interrelated nonseasonal variations at multiyear periods. El Niño episodes are characterized by intense turbulent mixing of the ocean by the wind, intense offshore-directed Ekman transport and by low net heat gain to the ocean through the sea surface. Effects of constant versus variable transfer coefficient formulations on the bulk aerodynamic flux estimates are discussed. Certain comments on the utilization of these data in analysis of biological effects are offered.

Introduction

By international convention, weather observations are recorded routinely on a various types of ships operating at sea. These maritime reports remain the primary source of information on large-scale variability in the marine environment. Even with the increasing development of satellite observation systems, analysis of time series of decadal length and longer must continue to depend heavily on these maritime reports for some time to come. Observations of wind speed and direction, air and sea temperature, atmospheric pressure, humidity and cloud cover included in these reports provide a basis for estimating a number of environmental variables pertinent to the study of variations in ocean climate and of effects of these variations on the associated communities of marine organisms. In this paper, the historical files of these observations are summarized to yield monthly estimates of properties and processes at the sea surface within the extremely productive upwelling ecosystem off central and northern Peru. The 32-year period treated encompasses several dramatic El Niño events and the spectacular rise, collapse, and indications of a recent rebound, of the largest exploited fish population that has ever existed, the Peruvian anchoveta.

Although remarkably rich both in biological productivity and in climatic scale ocean variability, the area off Peru is rather poor in maritime data density. Thus the region presents a particular challenge to the methodologies employed here. The area is very sparsely sampled in comparison to the corresponding eastern ocean boundary ecosystems of the northern hemisphere, with most of the reports coming from a narrow coastal shipping lane lying within about 200 km of the coast (Parrish et al. 1983). Maritime reports are subject to a variety of measurement and transmission errors, of which improper positioning is perhaps the most troublesome, sometimes introducing very large errors in all derived quantities (e.g., when a wrong hemisphere, etc., may be indicated). And it is difficult to establish effective procedures for rejecting erroneous reports without also suppressing indications of real variations, particularly in the area off Peru which is perhaps uniquely subject to drastic and abrupt natural environmental perturbations. For example, early indications of the 1982-1983 El Niño event went unnoticed by meteorological agencies in Europe and North America, because the reports which clearly indicated an event of unprecedented intensity were so far from the norm that they are rejected as erroneous by the automated data editing procedures (Siegel 1983). In addition, even when no actual errors are involved, irregular distribution of the reports in both time and space may introduce biases and nonhomogeneities into time series constructed from these data.

Tests of the precision of the methodology on interyear time scales, involving subsamplings of the much richer data distributions off the Iberian Peninsula in the northeast Atlantic Ocean, have indicated benefits to be gained by utilizing rather large areal samples, i.e., of the order of 10 degrees of latitude and longitude in extent, with the increase in report frequency overriding increases in sampling variance resulting from incorporation of additional spatial variability (Bakun, unpublished data). These same tests have indicated that the use of the ordinary 'standard error of the mean' provides a useful guide to the precision of monthly estimates, even though the underlying processes may be very highly variable on much smaller temporal and spatial scales than those used for data summarization. For the time series presented herein, reports available within an area extending some 10 degrees of latitude along the Peru coast and about 4 degrees of longitude offshore (Fig. 1), between Talara and a point just to the south of Pisco, were

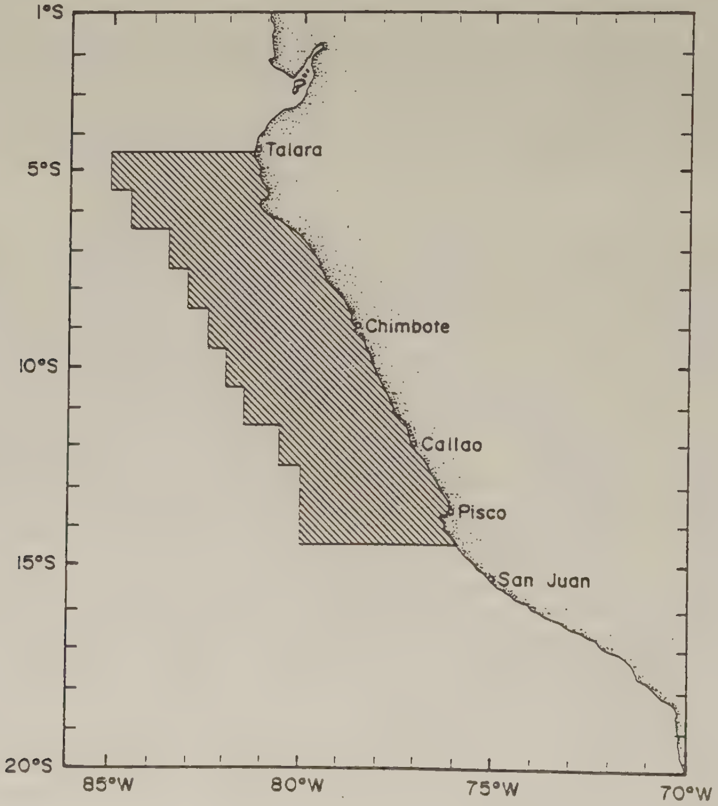

Fig. 1. Summary area. Maritime reports from within the area indicated by diagonal hatching were used for assembling monthly samples.

composited together. These composite samples are assumed to characterize temporal variability, at least in the relative sense, in conditions affecting the neritic fish habitat along that stretch of coastline which appears to have some degree of natural unity both in terms of environmental processes and biological community (Santander 1980; Parrish et al. 1983). The rather ragged offshore edge of the summary region was chosen to facilitate initial extraction of the reports from the data archive files. Consistent features of spatial variability tend to be much less intense in offshore areas of coastal upwelling regions than in coastal areas; thus no substantial effect of the irregularity of shape of the offshore boundary is expected. Also all the monthly summaries are treated identically in terms of areal selection and so time series homogeneity is preserved. In any case, report density is extremely low at the outer edge of the summary area.

Assembly of Data Series

Impossible or highly improbable values occur occasionally in the maritime report files, due to keypunch errors, etc. In the data record format, temperature values between -99.9 and 99.9°C are possible. Initial efforts to construct the data series resulted in rather large standard errors for certain of the monthly values due to incorporation of improbable data. For this reason, only values falling between the limits 11 to 31°C were accepted as valid observations of air temperature, sea surface temperature, or 'wet bulb' air temperature, for this region. (Note that the lower bound on the wet bulb temperature caused only 16 reports, no more than a single report in any one month, to be rejected). Wind speeds of up to 199 knots (102 m/sec) are possible in the record format. Erroneously high wind speeds have a particularly serious effect since wind speed is squared in the stress computation and cubed in the wind mixing index formulation. Reports of wind greater than 45 knots (23 m/sec) occurred within the summary region less than ten times in the entire 32-year record and were in no case corroborated by neighboring (in either space or time) data. Thus wind reports exceeding this value were excluded in preparing these time series. The data record format limited wind direction to values between 0 and 360 degrees, cloud cover observations to the range 0 to 100% of sky obscured, and barometric pressure to values between 890 and 1,070 millibars.

In assembling the monthly data samples, if any one of the reported values of sea surface temperature, barometric pressure, wind speed, or wind direction, were missing or unacceptable the entire report was excluded from the summaries. These four observed properties are sufficient to produce time series of sea surface temperature (Table 2), atmospheric pressure (Table 4), wind stress components (Tables 5 and 6), and wind mixing index (Table 7). The numbers of reports having acceptable observations of these four items are entered as the first of the three numbers shown for each month in Table 1. In addition, if a valid cloud cover observation was available the report was also incorporated in the cloud cover series (Table 3); numbers of reports including acceptable observations of these five items are entered as the second number of each monthly set in Table 1. Finally, if acceptable values of both air (dry bulb) temperature and either wet bulb or dew point temperature were included, the report was also used for construction of time series of atmosphere-ocean heat exchange components (Tables 8 to 11). Numbers of available reports containing acceptable observations of all seven properties required to construct all the time series presented in this paper are shown as the third number under each month in Table 1. All computations of derived quantities were performed on each individual report prior to any summarization process. A simple mean was taken as an estimate of the central tendency of each monthly sample. Computed standard errors of these mean values are displayed within the parentheses following each monthly value presented in the various data tables. An approximate 95% confidence interval estimate can thus be generated by multiplying the indicated standard error by the factor 1.96, and adding and subtracting the result from the monthly mean value (point estimate) to yield the upper and lower limits of the interval.

A small percentage of the reports contain wind observations in which the direction is noted as "variable"; i.e., no direction could be assigned. This properly occurs only when the wind speed is very low. In these cases the wind speed is used, as reported, in the calculations where it enters as a scalar quantity, i.e., in the calculations of wind mixing index, evaporative heat loss and conductive heat loss. In the computation of surface wind stress, wind enters as a vector quantity and directionality is crucial. Accordingly, for the surface wind stress calculations, variable winds are treated as calms. Because the wind speed enters the calculation as a "square", low wind values act essential as zeros in their effect on the monthly means, and so treating these weak variable wind observations as calms has no substantial effect. Also, the net effect of a stress from one direction is cancelled by an equal stress from the opposite direction, and so treating variable-directional stress as equivalent to calm conditions makes physical sense.

Sea Surface Wind Stress

Sea surface stress was estimated according to:

$$(\tau_x, \tau_y) = \rho_a C_D \left(|\vec{W}_{10}| U_{10}, \; |\vec{W}_{10}| V_{10} \right) \qquad \ldots 1)$$

where τ_x and τ_y are components of stress directed onshore and alongshore, respectively; a characteristic onshore direction of 62 degrees and an alongshore direction of 332 degrees (from true north) was assigned to the entire summary area. ρ_a is the density of air, considered constant at 1.22 kg/m^3. C_D is a dimensionless drag coefficient. $|\vec{W}_{10}|$ is the wind speed at 10 m height. U_{10} is the onshore-directed component of wind velocity; V_{10} is the alongshore-directed (positive equatorward) component. For the data series presented in the tables, C_D was considered to be a constant equal to 0.0013. The use of this constant drag coefficient has been a somewhat standard practice in climatological studies of upwelling regions (Bakun et al. 1974; Nelson 1977; Parrish et al. 1983). However, it is recognized that the value of the drag coefficient is actually a variable which depends on the nature of atmospheric turbulence near the sea surface. Thus a dependence on both atmospheric stability and wind magnitude near the sea surface is indicated; the stability effect is particularly important in reducing air-sea transfers in upwelling regions due to the stable atmospheric boundary layer formed over cool upwelled surface water. No clear consensus as to the proper formulation of these dependencies is presently available. However, a reasonable variable drag coefficient formulation has been chosen and has been applied to these data for evaluation of possible differences from results based on the constant drag coefficient formulation. In this case we follow the method of Nelson (1977) for incorporation of the atmospheric stability effect, which is based on a bulk Richardson number parameterization (Deardorff 1968). We incorporate a dependence on wind speed according to the recommendations of Large and Pond (1981) who find a linear increase in the drag coefficient at wind speeds greater than 11 m/sec.

Offshore Ekman Transport

In their climatological study of seasonality and geography of anchovy and sardine reproductive habitats within eastern ocean boundary upwelling systems, Parrish et al. (1983) found a pattern of minimization of both wind-driven offshore surface flow (Ekman transport) and of wind-induced turbulence in the spawning habits of these fishes. They therefore suggest the likelihood of important effects of both processes on reproductive success. Offshore Ekman transport at a given latitude is proportional to the alongshore stress, being simply the product of the alongshore stress and the reciprocal of the local Coriolis parameter. Ekman transport (Ekman 1905) provides an acceptable description of ocean surface transport directly driven by surface wind stress at periods which are long compared to the half-pendulum day; the half-pendulum day is 2.9 actual days in length at 10° latitude but increases to infinity at the equator. Obviously, the Ekman transport description cannot be applied directly at the equator. Here we assume the Ekman transport description to be adequate for the effect of wind stress variations affecting the summary area as a whole on the monthly time scale; thus we simply divide the monthly alongshore wind stress by a characteristic value of the Coriolis parameter (we choose the local value at 10°S, i.e., 0.0000253/sec, to characterize offshore Ekman transport in response to large-scale, long period wind variations over the anchoveta reproductive habitat; this choice will affect the average magnitude but not the time series properties of the resulting indicator series, which will be identical to those of the alongshore stress series).

Wind Mixing Index

The rate at which the wind imparts mechanical energy to the ocean to produce turbulent mixing of the upper water column is roughly proportional to the third power, or "cube", of the wind speed (Eisberry and Garwood 1978). A "wind mixing index", which is simply the mean of the cube of the observed wind speeds in each monthly sample (Table 7) is presented as a guide to longer period variability in this particular process. However, it is to be noted that these series may not reflect energetic shorter-term variability which may be more crucial to reproductive success of anchovies (Husby and Nelson 1982). The hypothetical basis for interest in this process in relation to anchoveta reproductive success is Lasker's (1978) suggestion that first-feeding success of anchovy larvae may be dependent upon availability of fine scale food particle concentrations which may be dispersed by wind-driven turbulent mixing events. These occur at atmospheric storm event scales which are much shorter than one month. Furthermore, it is not the exact magnitude of mixing that is crucial according to this hypothesis, but rather the existence of time-space "survival windows" within which the rate of addition of turbulence by the wind does not reach a level that homogenizes the food particle distributions (Bakun and Parrish 1980). The wind speed level at which this occurs and the minimum required duration of the window for substantial survival to result are unclear and undoubtedly are variable functions of other factors such as water column stability, the particular food particle organism's growth rate, behavior, motility, etc. In any case, the maritime reports occur irregularly in time and space and so are not amenable to indicating durations of periods characterized by specific conditions, even if we were able to specify the required nature of the conditions. This would require utilization of a time-and-space continuous meteorological analysis procedure (Bakun 1986) which might be ineffective due to the low maritime report density in the region and particularly seaward of the region. The use of shore station data, despite interference from local topographic influences, etc., might be the best available option for indicating short time scale wind variability over the ocean habitat off Peru (see Mendo et al., this vol.).

Solar Radiation

Net incoming solar radiation, Q_S, absorbed by the ocean was estimated according to the formula:

$$Q_S = (1 - \alpha)\, Q_o\, (1 - 0.62C + 0.0019h) \qquad \ldots 2)$$

where α is the fraction of incoming radiation reflected from the sea surface, Q_0 is the sum of the direct and diffuse radiation reaching the ground under a cloudless sky, C is the observed total cloud amount in tenths of sky covered and h is the noon solar altitude. For each maritime report, the total daily direct solar radiation reaching the ground under cloudless conditions was extracted from the Smithsonian Meteorological Tables (List 1949) as a function of the date and latitude of the report, using a 4 x 4 element curvilinear interpolation on the table entries via Bessel's central difference formula and assuming the atmospheric transmission coefficient of 0.7 recommended by Seckel and Beaudry (1973). The diffuse solar radiation was estimated according to List's recommendations as follows. The solar radiation reaching the top of the atmosphere was extracted from the appropriate table. This value was decreased by 9% to allow for water vapor absorption and 2% for ozone absorption. The result is subtracted from the value previously determined for the direct radiation reaching the ground to yield the energy scattered out of the solar beam. This is reduced by 50% (to reflect the fact that half is diffused upward and therefore only half is diffused downward) to yield the total diffuse solar radiation reaching the ground. The total daily direct and diffuse radiation values corresponding to each report are then summed to yield Q_S. The remainder of the computation follows the procedures adopted by Nelson and Husby (1983). The linear cloud correction in Equation (2) is as suggested by Reed (1977), and Reed's recommendation that no correction be made for cloud amounts less than 0.25 of total sky was followed. Sea surface albedo was extracted from Payne's (1972) tables, following Nelson and Husby's (1983) algorithm which consists of entering the tables with the 0.7 atmospheric transmission coefficient reduced by a factor equal to the linear cloud correction applied in Equation (2) and the mean daily solar altitude. The possible error in the net radiation estimate introduced by using the mean daily solar altitude to indicate albedo, rather than an integration over the entire day of entries at short time intervals with instantaneous solar altitudes, is estimated to be of the order of 1%.

Radiative Heat Loss

Effective back radiation is the difference between the outgoing long-wave radiation from the sea surface, which depends on the 4th power of the absolute temperature of the sea surface, and the incoming long-wave radiation from the sky, which depends on the water vapor content of the atmosphere and on the nature of the cloud cover. Here we follow exactly the computational scheme of Nelson and Husby (1983) who used the modified Brunt equation (Brunt 1932) with the empirical constants of Budyko (1956) and the linear cloud correction formula of Reed (1976) to compute the effective back radiation (radiative heat loss), Q_B:

$$Q_B = 5.50 \times 10^{-8} (T_S + 273.16)^4 (0.39 - 0.05 e_a^{1/2}) (1 - 0.9C) \qquad \ldots 3)$$

The vapor pressure of the air, e_a, was computed according to the formula provided in the Smithsonian Meteorological Tables (List 1949) using the observed barometric pressure, and "dry bulb" and "wet bulb" air temperatures. For reports that were without an acceptable wet bulb temperature but included an acceptable dew point temperature, the vapor pressure was computed as the saturation vapor pressure at the dew point temperature using an integrated form of the Clausius-Clapeyron equation (Murray 1967).

Evaporative and Conductive Heat Losses

In estimating evaporative heat loss (latent heat transfer) and conductive heat loss (sensible heat transfer), the procedures of Nelson and Husby (1983) are again followed closely, except for a modification of the wind speed dependence in their variable transfer coefficient formulations as indicated below. The bulk aerodynamic formula for turbulent fluxes of latent and sensible heat across the air-sea interface in a neutrally stable atmospheric boundary layer (Kraus 1972) can be expressed as

$$Q_E = \rho_a L C_E (q_0 - q_{10}) |\vec{W}_{10}| \qquad \ldots 4)$$

$$Q_C = \rho_a c_p C_H (T_3 - T_a) |\vec{W}_{10}| \qquad \ldots 5)$$

where ρ_a and $|\vec{W}_{10}|$ are as in Equation (1), with ρ_a assigned the same constant value (1.22 kg/m^3) as in the stress computation. L is the latent heat of vaporization, assigned a constant value of 2.45 x 10^6 J/kg (585.3 cal/gm). c_p is the specific heat of air, assigned a constant value of 1,000 J/kg/^{o}C (0.239 cal/g/^{o}C). The empirical exchange coefficients, C_E and C_H, were assigned constant values of 0.0013 in the construction of the time series presented in Tables 10 and 11. In addition, time series based on variable transfer coefficient formulations incorporating dependencies on atmospheric stability and on wind speed were also assembled for comparison. These formulations are again those chosen by Nelson and Husby (1983) which incorporate the atmospheric stability effect according to a bulk Richardson number parameterization (Deardorff 1968); however, Nelson and Husby's wind speed dependencies were in this case modified according to the recommendations of Large and Pond (1982) who suggest an increase in C_E and C_H which is proportional to the square root of the wind speed. The specific humidities of the air in contact with the sea surface, q_0, and at 10 m or deck level, q_{10}, were computed according to

$$q \approx E\frac{e}{P} \qquad \ldots 6)$$

where E is the known ratio (a constant equal to 0.622) of the molecular weight of water vapor to the net molecular weight of dry air, *e* is the vapor pressure and P is the barometic pressure. For this calculation the variation in P is negligible and so a constant value of 101.325 pascals (1,013.25 mb) was assigned. The calculation of *e* at 10 m, or deck level, is as indicated for the radiative heat loss calculation (Equation 3). To calculate *e* at the sea surface, the saturation vapor pressure over pure water was computed from a formula given by Murray (1967), and reduced by 2% to account for the effect of salinity (Miyake 1952).

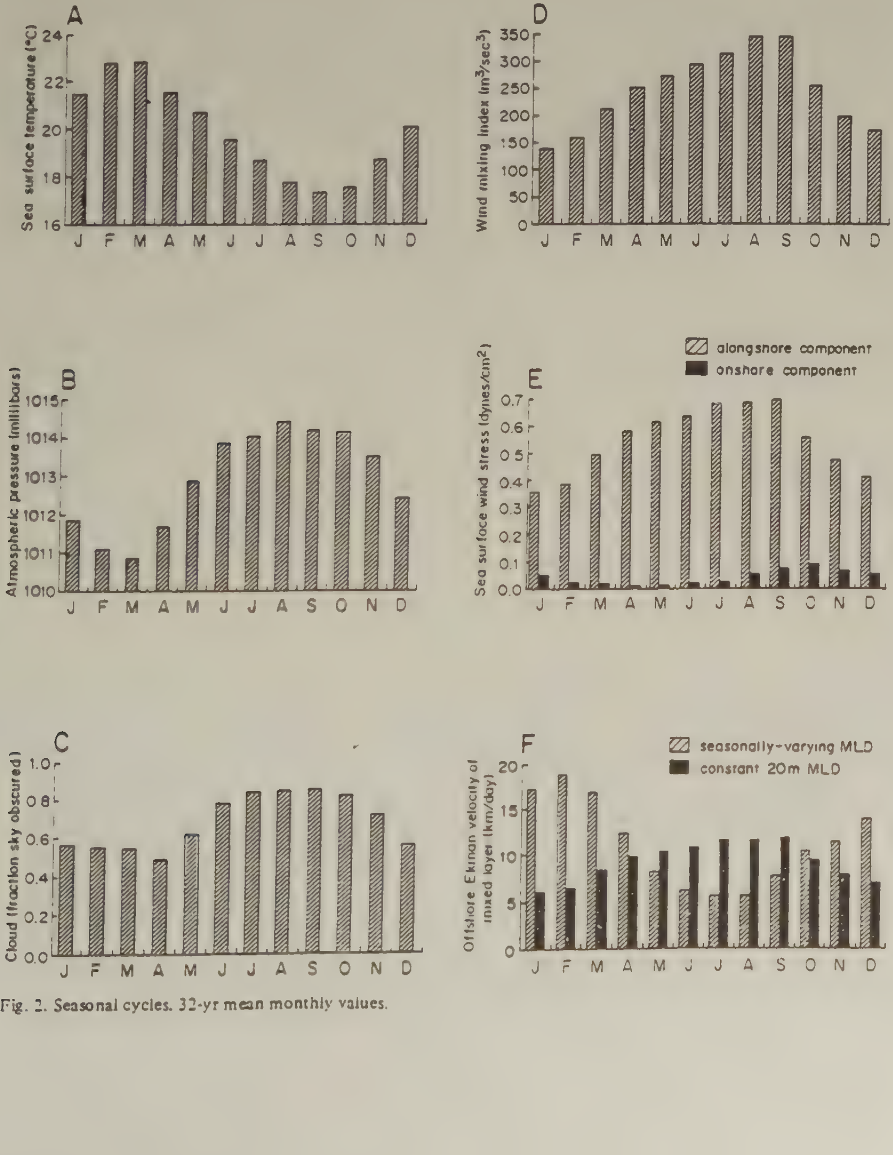

Fig. 2. Seasonal cycles. 32-yr mean monthly values.

The Seasonal Cycles

The idea of regular seasonal cycles for the coupled ocean-atmosphere system off Peru is to some degree illusory in view of the predominant influence of interyear variability in the region. However, the seasonal variation is the most cyclic and predictable of the large components of variability. It is therefore the component of variation which is most likely to be reflected in biological adaptations. Accordingly, a summary of the long-term mean monthly values of the various series (Figs. 2 and 3) serves as a useful starting point for discussion.

Being situated within the tropical band, the region experiences two passages of the sun each year; the sun is directly overhead in October and again in February-March. Also, since the earth's meteorological equator is displaced to the north of the geographical equator, the region is dominated by southern hemisphere atmospheric dynamics; thus austral winter dominates the seasonality of transfers of momentum and mechanical energy from atmosphere to ocean.

The 32-year mean monthly sea surface temperature (Fig. 2A) is at a maximum in March, coinciding with the second period of vertical sun which marks the culmination of the extended austral summer period of relatively high sun. The temperature falls to a minimum in August. The atmospheric pressure (Fig. 2B) tends to be directly out of phase, being at a minimum in the austral summer and at a maximum in the winter season. Cloudiness (Fig. 2C) lags the atmospheric pressure variation by about one month. On average less than 50% of the sky is obscured by clouds in April; this increases to greater than 85% in September.

The strength of the wind exhibits a typical southern hemisphere seasonality, being strongest in austral winter and weakest in summer. Thus the 32-year mean monthly values of the index of rate of addition of turbulent mixing energy to the water column (Fig. 2D) reach a maximum in August-September and a minimum in January. The fact that the seasonal spawning peak of anchoveta is centered within this August-September turbulent mixing maximum would indicate non-adaptation of reproductive strategy for minimization of turbulent mixing effects. This is not in accordance with the general pattern suggested by Parrish et al. (1983) as generally characterizing seasonality and geography of spawning of eastern ocean boundary anchovy populations. Although no claim is made for conclusiveness, the inference would seem to be that Lasker's (1978) hypothesis is not, at least in most years, the major factor affecting anchoveta reproductive success off Peru. Note that the level of turbulent mixing index intensity off Peru is low compared to other anchovy reproductive habitats, even at its seasonal maximum.

The alongshore component of wind stress on the sea surface is consistently equatorward: in no case in the 32-year series (Table 5) did any monthly wind mean stress value deviate from this predominently alongshore and equatorward tendency in the transfer of momentum from atmosphere to ocean. The long-term mean values of alongshore stress (Fig. 2E) follow the same seasonal pattern as the turbulent mixing index, reaching a maximum in September and a minimum in January. The 32-year mean monthly values of the onshore component of stress are small compared to those of the alongshore component, but are positive (onshore-directed) at all seasons.

Surface Ekman transport, being proportional to the alongshore stress but directed perpendicularly to the left of the stress, is thus directed offshore, with a seasonal maximum again corresponding to the seasonal spawning peak of anchoveta. This "anomaly" to the pattern of apparent minimization of offshore transport in spawning strategies of engraulids puzzled Bakun and Parrish (1982). However, Parrish et al. (1983) showed that the seasonal variation in mixed layer depth off Peru proceeds in phase with that of transport, in response to the seasonalities in turbulent mixing (Fig. 2C) and surface cooling (Fig. 2A), but has greater relative amplitude. The result is that drifting organisms which are distributed through the upper mixed layer would experience a faster net offshore drift in the thinner surface mixed layer of austral summer than in the deeper mixed layer of winter, even though the winter transport (by volume) is much larger. This is illustrated in Fig. 2F, which shows calculations of mean monthly offshore Ekman velocity of the mixed layer performed in two different ways (based on the 32-year mean monthly values of the data presented in Table 5). Firstly, the monthly estimates of offshore Ekman transport are divided by the composite mean (20 m) of the mixed layer depth values given for 2-month segments of the seasonal cycle by Parrish et al. (1983). Secondly, the same monthly estimates of offshore Ekman transport are divided by monthly mixed layer depth estimates produced by curvilinear interpolation of the 2-month seasonal segments. The effect of variable mixed layer depth on the net offshore velocity is apparent, and suggestive of adaptation of spawning seasonality for avoidance of offshore loss of larvae (for additional discussion of this aspect, see Bakun 1985). The effect of the choice of a constant or variable drag coefficient formulation in the stress computation (Equation 1) on the seasonal signal is indicated in Fig. 3A. The 32-year mean monthly Ekman transport values based on the variable coefficient formulation follow a seasonal progression which is very similar to those based on the constant coefficient formulation (i.e., presented in Table 5); however they are slightly smaller in magnitude, reflecting the effect of stability in the atmospheric boundary layer which is stabilized as the onshore-directed airflow is cooled from below while traversing the coastal upwelling zone.

Solar radiation entering the ocean (Q_S) is at a maximum during the February overhead passage of the sun (Fig. 3B). This is due to substantially reduced cloud cover relative to the November solar passage. Solar radiation is at a minimum in July, when solar altitude has just passed its June minimum, and cloudiness is approaching its winter maximum.

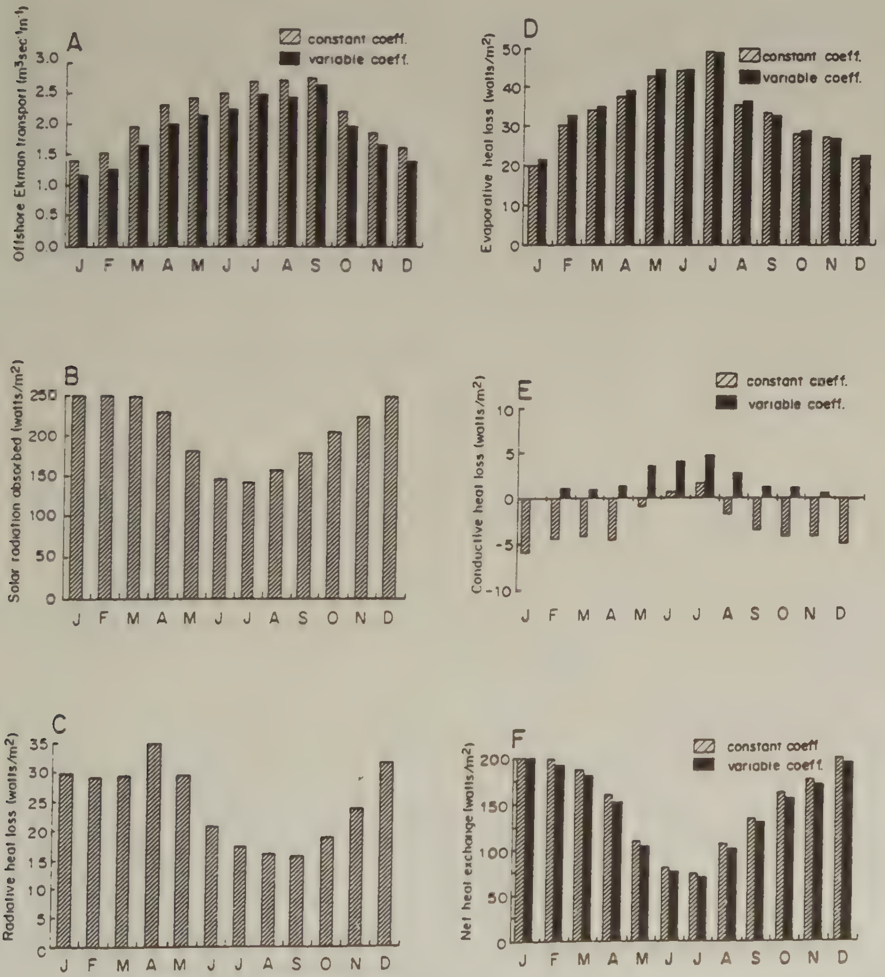

Fig. 3. Seasonal cycles. 32-yr mean monthly values. (Note that the SI-standard heat flux units, watts per square meter, may be converted to calories per square centimeter per day by multiplying by the factor 2.604)

Heat loss from the sea surface via long-wave radiation (Q_B) is only a small fraction of the short-wave radiation absorbed reflecting the area's location within the tropical band (Fig. 3C). Radiative heat loss is at a seasonal maximum during April, corresponding to the minimum in cloudiness, and at a minimum in September, corresponding to the cloudiness maximum.

Heat loss from the ocean via evaporation at the sea surface (Q_E) is at a maximum during austral winter and at a minimum during summer (Fig. 3D). The choice of constant or variable transfer coefficient has only a slight effect, with the results of the variable coefficient formulation appearing to increase very slightly in magnitude relative to those of the constant coefficient formulation toward the summer and fall seasons.

Heat loss via conduction (Q_C) is very small compared to the other heat exchange components (Fig. 3E). This is fortunate because the choice of transfer coefficient formulation completely changes the seasonal pattern. With the constant coefficient formulation, conductive heat loss is mostly negative, indicating heating of the ocean surface by contact with the atmosphere. This reflects the common situation of cool upwelling-affected surface waters being in contact with a generally warmer atmosphere. However, the strong stability of the atmosphere boundary layer inherent in this situation inhibits conductive heat transfer according to the variable transfer coefficient formulation. Thus the less common situation where the air is cooler than the water dominates the sensible heat transfer according to the variable coefficent formulation, with the result that conductive heat loss is indicated as being positive in all the 32-year composite monthly means except the summer months of January and February.

The 32-year monthly means of the time series of atmosphere-ocean heat exchange (Q_N), which represent the resultant differences between the amount of solar radiation absorbed by the ocean and the sum of the heat losses due to long-wave radiation, evaporation and conduction, indicate substantial heat gain by the ocean throughout the year (Fig. 3F). As expected, the average heat gain is greatest in austral summer, reaching values of the order of 200 watts/m^2 (413 cal cm^{-2} day^{-1}) in January, and least in winter, falling to about 70 watts/m^2 (144 cal cm^{-2} day^{-1}) in July. The constant coefficient formulations yield slightly greater numerical values of net heat exchange than do the variable coefficient formulations, mainly due to the differences in the respective indications of the conductive heat loss component discussed in the previous paragraph; however the respective seasonal progressions are very similar.

Interyear Variations

If cyclical seasonal effects are those most likely to be adapted for and incorporated in life cycle strategies of organisms, major nonseasonal variations are those most likely to cause disruptions in life cycle processes and therefore to be reflected in population variations. Very short-scale nonseasonal variations are not well resolved in these monthly composites of irregularly distributed maritime reports. However, when shorter period variability is smoothed and the cyclic seasonal effects are suppressed, nonseasonal variations of longer than annual period, which represent substantial perturbations of the environmental "normalcy" to which reproductive strategies or other life cycle strategies should have become tuned, are clearly manifested. For the purposes of this discussion, a simple 12-month running mean filter is chosen to suppress seasonalities and smooth the higher frequencies.

Problems (negative side lobes, wavelength-dependent phase shifts, etc.) with such equally-weighted moving average filters are well known (Anon. 1966). However, in this case the alternatives also present problems. We particularly wish to suppress the seasonal cycle, and so weighting the filter elements to suppress side lobes at other frequencies while increasing leakage of the seasonal frequency, is not desirable. Smoothed monthly series of anomalies from long-term monthly means (e.g., Quinn et al. 1978; McLain et al. 1985) have the property that the filtering is "nonlocal", i.e., that any value is dependent on other values in the same calendar month in temporally "distant" parts of the time series. Thus, for example, an intense warming (e.g., El Niño) occurring within a generally cool climatic period appears as a much less intense anomaly than a warming of similar magnitude within a warm period; also, the degree of indicated intensity changes whenever the length of the series used for determination of the long-term mean changes. More importantly, if the amplitude (or shape, phase, etc.) of the seasonal variation is undergoing nonseasonal variation, taking anomalies introduces spurious seasonal-scale variations into the filtered series. A "local" seasonal filter that avoids some of these problems can be based on 12th-differences. e.g., the result of subtracting from each monthly value the value for the same calendar month in the previous year, but the result is thereby transformed to annual rates of change of a property rather than the property itself, which complicates a descriptive discussion. However, the use of 12th-difference transforms is worth considering for empirical modelling efforts. For the purposes of this discussion, the simple 12-month running mean provides a "local" seasonal filter/smoother which will be familiar to many readers and adequate for a descriptive treatment.

The filtered sea surface temperature series (Fig. 4A) illustrates well the major El Niño warm events of the period: 1957-1958, 1965, 1969, 1972-1973, 1976 and 1982-1983. Generally elevated temperatures in the period between the 1976 and 1983 events are also apparent. Also apparent is the extended cold period of the mid-1950s: the indication of rise in temperature from this cold period to the peak of the 1957-1983 El Niño is comparable in total magnitude to that of the rise of the 1982-83 El Niño from the much warmer climatic base temperature level of the late 1970s.

Major features in the filtered cloud cover series (Fig. 4B) are visibly related to those in the temperature series, but not in any simple, consistent manner. Cloud cover minima often appear to coincide with the relaxation of El Niño events. An extraordinarily low degree of cloudings appears to have coincided with the return to normal sea temperatures in 1984. Another sharp cloud cover minimum coincided with the leveling off of the temperature decline following the 1957-1958 event. Likewise cloud cover maxima often appear to coincide with rapid drops of temperature into cool periods. Atmospheric pressure variations (Fig. 4C) are obviously highly inversely correlated, at these low frequencies, with those of sea surface temperature.

It is not surprising, in view of the dynamic linkage of wind to horizontal gradient of atmospheric pressure, that wind variations would be related to those of atmospheric pressure. The relation of the "wind-cubed" index of rate of addition of turbulent mixing energy to the ocean by the wind (Fig. 4D) to El Niño periods is striking. El Niño events are evidently strong wind-mixing events which, according to Lasker's (1978) scenario, would correspond to periods of high probability of starvation for first-feeding anchoveta larvae. The period during and immediately following the 1972 El Niño appears to have been characterized by an extended period of highly turbulent upper water column conditions. The period during and following the 1982-1983 event appears to have been similarly turbulent, except for a 2-month "window" of relaxed turbulent mixing index during December 1983 and January 1984 (somewhat masked by the smoothing in Fig. 4C, but evident in the unsmoothed monthly values in Table 7).

The magnitude of alongshore (equatorward) wind stress also increases during El Niño events (Fig. 4E), in agreement with Wyrtki's (1975) conclusions which were based on a summary area displaced somewhat southward along the coast (10-20°S, 70-80°W) from the one used here (Fig. 1). Thus in addition to potential increases in larval starvation due to increased destruction of food particle strata by turbulent mixing, an increase in potential offshore loss of larvae from the favorable coastal habitat is also indicated. The onshore component of surface wind stress is relatively small and consistently positive (onshore-directed) in the filtered series.

In the previous section, the effect of seasonally-varying mixed layer depth on the offshore Ekman velocity of particles which are continually mixed through the upper mixed layer was discussed (i.e., in reference to Fig. 2F). To investigate the effect on interyear time scales, filtered time series of offshore Ekman velocity were calculated as in that section, i.e., (i) assuming a constant MLD of 20 m and (ii) assuming a seasonally varying MLD derived from the values given by Parrish et al. (1983). The result indicates that, at least for the MLD values chosen, the effect of seasonally-varying mixed layer depth is such as to substantially increase on average the rate of offshore movement of passive particles in the mixed layer. If the effective mixed layer depth is increased during El Niño, as would be expected both from the effect of the propagating baroclinic wave in deepening the surface layer and also from the enhanced wind induced turbulent mixing, the effect would be to counteract the increased rate of offshore movement indicated from the Ekman transport calculations.

The effect of the choice of constant or variable drag coefficient formulation in the stress computation (Equation 1) is illustrated in Fig. 4G, where the alongshore stress variation is

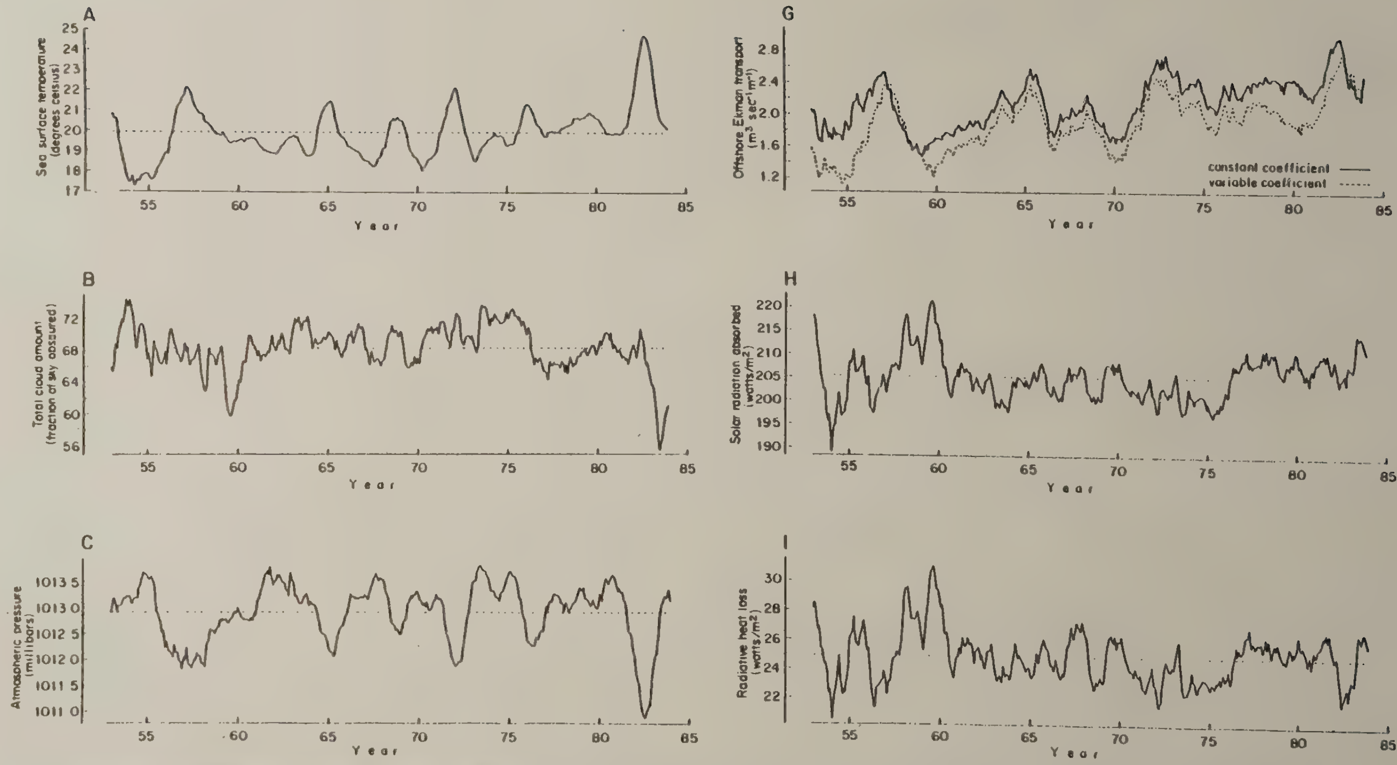

Fig. 4. Low-frequency nonseasonal variations, 12-month running means of monthly time series values. (Note that the SI-standard heat flux units, watts per square meter, may be converted to calories per square centimeter per day by multiplying by the factor 2.064.)

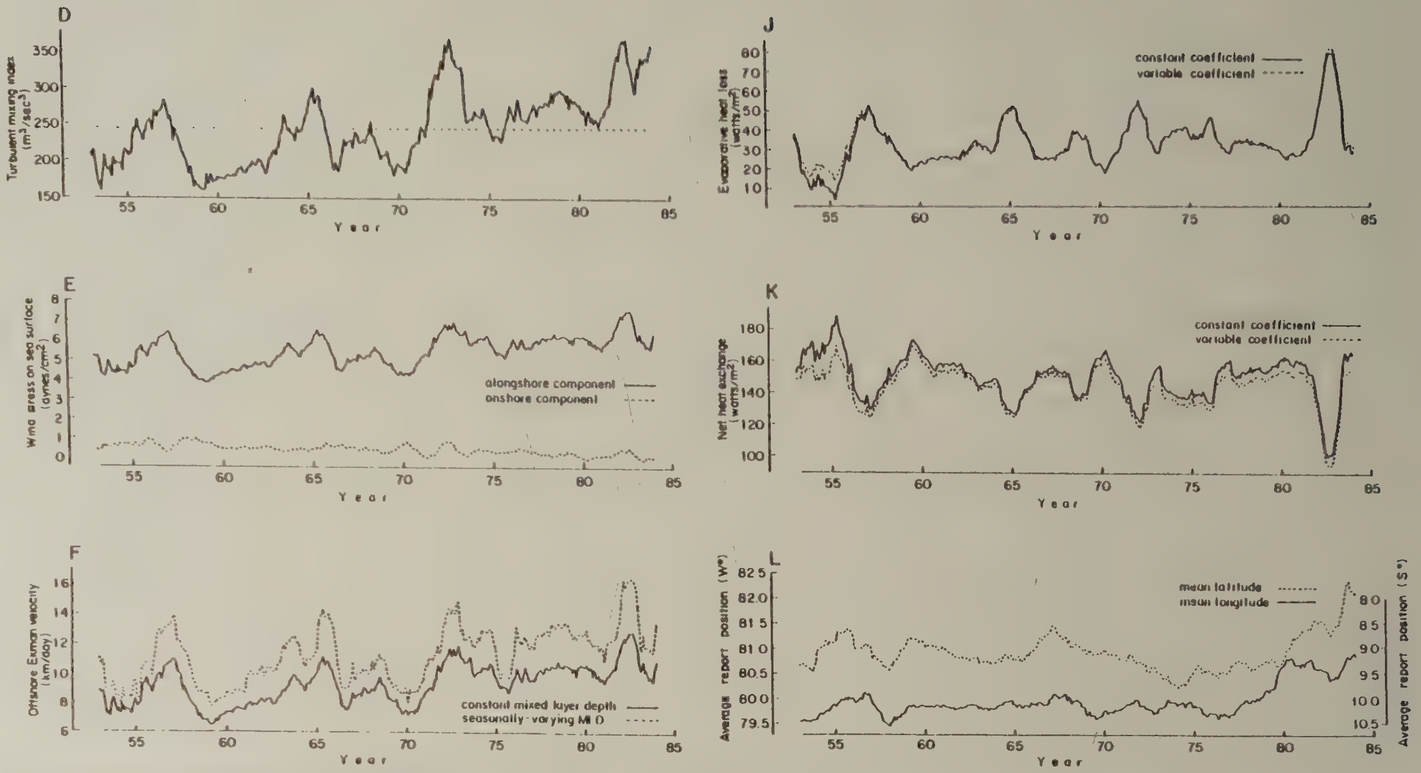

Fig. 4. Continued. Low-frequency nonseasonal variations, 12-month running means of monthly time series values. (Note that the SI-standard heat flux units, watts per square meter, may be converted to calories per square centimeter per day by multiplying by the factor 2.064.)

plotted in terms of its directly proportional transform, offshore Ekman transport. The variable coefficient formulation produces generally lower estimates of stress due to the influence of the stability of the lower atmospheric boundary layer over upwelling-affected surface waters. However the differences essentially disappear during the period of relaxation of the intense El Niños of 1957-1958 and 1982-1983. A possible explanation is the tendency for a less stable atmosphere in contact with the ocean surface due to residual warmth which would linger longer in the ocean than in the atmosphere due to the much greater heat storage capacity of water compared to that of air.

The filtered series of estimates of absorption of solar radiation by the ocean (Q_S) exhibits some interesting patterns (Fig. 4H). Since the variables that control the solar radiation estimate (Equation 2) derived from a maritime report at any given latitude are calendar date and cloud cover, it is not surprising that maxima in Fig. 4H often correspond to minima in Fig. 4B, and vice versa. However there are discernible differences between the two series that result from the interaction of the cloud cover variations with the seasonal changes in solar height in the solar radiation time series. An impressive feature in the solar radiation series is the early large-amplitude alternation consisting of deep minimum of solar radiation entering the ocean corresponding to the early part of the intense 1954-1955 cold period, followed by a sharp, highly erratic rise to a high peak in early 1960. In addition, the entire period of the 1960s and the first half of the 1970s appears to have been characterized by low absorption of solar radiation relative to the more recent period since 1976.

The long-wave radiative heat loss (Q_B) tends to be an order of magnitude smaller than the short-wave absorption, but varies very similarly (Fig. 4I). This similarity is perhaps explainable in the similar dependence of both types of estimate on cloud cover, with the sea surface temperature dependence in the long-wave radiation estimate (Equation 3) being related seasonally to the solar height dependence in the solar radiation estimate (Equation 2). There may also be some actual causal effect of the long period variations in solar radiation on the sea temperature dependence in the long-wave radiation estimate.

The filtered series of evaporative heat loss (Q_E) delineates the various El Niño episodes and the 1954-1955 cold period, in a very similar fashion to the sea surface temperature series (Fig. 4J). The long-term variation in vapor pressure difference between the sea surface and the overlying atmosphere (Equation 4) is apparently very closely linked to that of sea surface temperature. As discussed above, the wind speed dependence is also a strong function of these climate scale events. The effect of choice of constant or variable transfer coefficient apparently makes very little difference, except during the mid-1950s cold period, where increased stability of the air over the cold ocean apparently inhibited the turbulent exchange of latent heat according to the variable coefficient formulation.

The net ocean-atmosphere heat exchange series (Q_N) indicates long-term variations in net ocean heat gain such that minima are associated with El Niño episodes and maxima with cold periods. The variations appear to be controlled to a substantial extent by the evaporative heat loss (Fig. 4J). This is so because the variations in heat gain by absorption of short-wave solar radiation (Fig.4H) are partially offset by the highly correlated variations in long-wave radiative heat loss (Fig. 4I). The net effect of the choice of variable or constant transfer coefficient formulations in the evaporative and conductive components is a slight general lowering of the magnitude of net heat gain in the variable coefficient case. This difference is due primarily to the stability effect on the conductive heat loss term, as discussed in the previous section in reference to Fig. 2E, where the average change in the mean net value of this component, approximately 5 watts/m^2, corresponds in general to the approximate difference between the curves in Fig. 4K, except in the mid-1950s where stability effects on the evaporative heat loss term are appreciable.

In order to check for long-period variations in the distribution of observations within the summary area (Fig. 1), filtered series of the monthly averages of the respective latitudinal and longitudinal locations of reports were prepared (Fig. 4L). Since the coastline is oriented somewhat northwest to southeast, variations in the two curves which tend to parallel each other in the figure, will tend to yield a resultant displacement in the alongshore direction. More serious with respect to the long-term homogeneity of the monthly series herein presented are variations in Fig. 4L where the curves are changing in the opposite sense, i.e., where the net displacement of the mean position of reports is in the onshore-offshore direction; these situations are

Table 1. Numbers of observations in monthly samples used to construct time series. For each month the first number refers to observations used in constructing the values in Tables 2,4,5,6 & 7 (sea temperature, atmospheric pressure, wind stress components, and "wind cubed" index; the 2nd number refers to observations used in constructing the values in Table 4 (cloud cover); the 3rd number refers to observations used for values in Tables 8,9,10 & 11 (heat exchange components).

	Jan			*Feb*			*Mar*			*Apr*			*May*			*Jun*		
1953	21	19	19	29	29	29	22	22	19	23	23	10	33	33	33	16	16	6
1954	61	57	40	19	19	17	21	21	21	59	59	53	42	39	39	36	34	24
1955	24	22	20	35	35	29	16	15	12	9	9	5	24	24	13	35	35	30
1956	41	38	15	17	15	15	16	16	3	39	39	21	22	22	16	20	20	7
1957	32	32	32	25	24	15	98	98	47	38	38	29	25	25	21	53	52	33
1958	153	153	106	74	73	44	69	69	34	84	84	28	67	66	44	110	107	52
1959	128	125	51	162	162	49	143	138	37	115	112	37	97	96	21	67	67	43
1960	98	95	42	148	146	110	166	166	105	151	146	101	171	164	135	85	82	59
1961	148	147	127	124	124	90	115	111	94	183	180	150	89	86	66	130	128	104
1962	185	183	127	149	148	134	163	162	142	157	155	122	114	111	105	177	177	147
1963	78	76	71	103	102	102	182	181	167	180	177	170	157	156	149	185	185	185
1964	129	129	98	138	137	135	82	81	81	76	76	76	45	45	45	52	52	52
1965	59	59	58	75	71	70	137	137	137	99	99	96	139	136	136	139	139	138
1966	107	107	107	82	82	82	113	112	111	106	106	106	117	113	110	137	137	137
1967	111	109	102	60	52	52	80	80	78	147	144	144	75	74	74	66	66	66
1968	76	76	76	128	127	127	108	108	108	139	137	137	91	87	87	111	109	108
1969	67	67	67	87	84	84	134	131	131	91	91	91	56	56	56	102	102	102
1970	90	87	82	57	57	53	103	100	90	51	51	48	99	98	92	208	206	200
1971	103	101	93	81	77	75	89	89	89	53	53	52	44	44	44	22	22	21
1972	109	108	104	54	52	51	49	49	47	85	85	85	81	81	81	56	56	56
1973	55	54	40	44	44	39	89	89	89	50	50	48	58	58	56	57	54	47
1974	84	78	78	63	63	58	113	109	100	57	54	54	119	118	117	73	72	72
1975	59	57	56	73	72	69	140	140	140	99	92	90	140	138	136	116	115	114
1976	70	69	68	20	19	19	76	73	71	59	59	55	71	71	70	49	44	40
1977	51	51	51	109	106	105	79	79	73	101	99	94	93	88	87	70	70	69
1978	57	56	56	65	65	62	71	69	67	92	92	88	71	71	71	41	40	35
1979	97	96	89	58	57	51	105	104	98	85	85	77	83	80	74	48	45	34
1980	96	93	80	106	105	93	125	123	102	75	70	54	151	146	119	246	201	98
1981	116	113	85	90	89	82	139	137	124	108	103	95	115	108	79	128	124	108
1982	91	89	82	90	90	80	152	146	139	100	98	88	103	98	80	54	54	41
1983	68	64	54	126	126	116	94	91	86	76	72	61	93	92	83	61	61	55
1984	90	75	26	99	80	39	90	59	14	75	41	16	58	39	6	56	49	29

	Jul			*Aug*			*Sep*			*Oct*			*Nov*			*Dec*		
1953	10	10	9	39	35	26	29	28	25	18	18	11	24	24	18	19	18	11
1954	40	39	38	14	14	10	27	26	22	46	43	37	30	30	6	18	18	9
1955	17	17	12	37	36	21	35	35	6	45	44	34	27	27	20	13	13	5
1956	45	45	36	21	21	21	29	29	21	41	40	29	63	61	20	24	24	6
1957	27	27	11	24	24	21	64	64	38	112	110	65	100	99	53	115	115	86
1958	51	51	27	159	159	83	96	93	44	113	108	47	115	110	63	58	43	26
1959	100	100	57	103	101	39	85	81	42	74	74	21	110	110	55	114	114	85
1960	169	168	147	114	111	67	142	142	94	75	75	46	63	63	23	82	81	59
1961	108	107	82	155	155	142	153	151	141	128	127	80	197	197	192	135	133	118
1962	213	212	193	168	168	159	81	81	75	129	125	125	173	172	152	91	88	79
1963	120	120	120	70	70	70	110	110	101	70	70	70	61	61	58	56	56	53
1964	90	88	87	71	65	64	94	94	88	129	127	121	62	61	58	105	104	102
1965	92	92	92	119	117	115	99	99	98	67	67	67	177	176	176	111	111	106
1966	116	112	112	122	118	118	185	182	182	131	125	125	89	89	88	123	123	123
1967	89	87	87	67	67	67	84	84	84	76	71	71	73	73	73	99	97	97
1968	58	58	58	82	81	81	59	59	56	111	109	108	118	118	118	66	65	65
1969	70	70	70	86	84	84	108	97	92	102	102	97	137	137	127	101	101	96
1970	75	74	74	66	65	65	91	90	90	50	50	50	127	125	124	68	68	67
1971	43	43	42	58	58	54	28	28	23	51	51	47	78	78	78	34	31	30
1972	35	32	30	60	58	54	32	32	29	81	74	74	31	28	26	51	51	48
1973	81	75	74	105	92	88	89	84	82	55	54	50	100	98	98	71	71	70
1974	102	101	101	90	89	89	67	66	66	53	52	50	78	78	77	44	44	44
1975	67	66	65	53	48	47	70	68	68	70	65	60	68	68	67	88	88	88
1976	74	74	72	21	21	18	88	87	86	76	76	73	46	44	44	58	57	57
1977	55	54	53	55	51	51	73	70	68	106	104	104	183	166	163	67	59	59
1978	37	33	30	55	51	50	73	72	67	53	49	49	99	79	76	87	87	85
1979	80	75	63	117	108	90	116	109	82	84	77	53	77	75	59	39	35	26
1980	281	233	53	207	182	90	148	131	94	129	118	89	80	74	61	70	66	47
1981	169	161	78	174	159	63	122	111	92	127	115	97	174	155	142	154	147	127
1982	78	74	68	78	70	66	71	62	55	106	102	81	132	124	113	93	89	51
1983	124	121	84	145	116	46	70	48	19	156	150	90	73	73	24	96	90	32
1984	104	90	41	113	95	65	87	69	8	75	54	25	62	40	14	77	61	35

Table 2. Sea surface temperature in degrees Calsius. The standard error of the mean appears within parentheses to the right of the mean temperature value.

	Jan	Feb	Mar	Apr	May	Jun
1953	21.14(.50)	23.08(.64)	24.63(.51)	24.78(.49)	22.79(.37)	20.52(.46)
1954	18.55(.33)	22.86(.46)	22.01(.42)	16.36(.29)	17.86(.23)	16.95(.25)
1955	21.72(.39)	18.50(.52)	21.01(.85)	19.01(.37)	17.89(.85)	16.67(.30)
1956	19.90(.44)	17.64(.82)	21.66(.46)	20.71(.29)	19.90(.41)	19.22(.29)
1957	19.47(.47)	24.83(.48)	25.26(.21)	24.53(.37)	24.76(.48)	23.15(.27)
1958	23.15(.11)	25.00(.19)	24.52(.25)	22.83(.30)	21.63(.35)	20.42(.18)
1959	20.45(.21)	23.08(.18)	24.49(.15)	21.54(.25)	20.90(.18)	19.26(.25)
1960	21.97(.18)	22.74(.18)	22.70(.19)	20.58(.18)	19.09(.14)	18.22(.18)
1961	22.30(.15)	23.24(.20)	21.61(.21)	19.94(.15)	20.24(.21)	18.67(.15)
1962	21.29(.14)	22.12(.18)	20.37(.18)	19.41(.18)	18.68(.18)	18.92(.12)
1963	20.72(.24)	22.67(.17)	22.15(.16)	20.21(.17)	21.01(.13)	18.98(.10)
1964	21.44(.12)	22.41(.14)	20.91(.22)	20.66(.37)	18.38(.26)	17.35(.24)
1965	21.75(.26)	23.09(.27)	23.96(.15)	24.54(.21)	24.08(.20)	22.11(.14)
1966	22.09(.20)	23.62(.20)	21.96(.25)	20.85(.24)	19.88(.24)	18.67(.16)
1967	20.01(.22)	22.12(.22)	21.86(.23)	20.61(.19)	19.11(.24)	18.13(.30)
1968	19.67(.21)	22.21(.21)	21.78(.22)	18.60(.20)	18.49(.30)	17.31(.20)
1969	22.28(.23)	22.36(.23)	24.25(.18)	23.51(.23)	22.94(.25)	20.92(.22)
1970	21.71(.26)	21.94(.43)	22.51(.26)	20.40(.33)	18.73(.21)	16.85(.14)
1971	19.70(.19)	20.34(.29)	19.70(.25)	21.63(.36)	19.80(.32)	18.46(.46)
1972	20.94(.25)	24.38(.41)	25.17(.37)	22.97(.24)	23.05(.22)	21.68(.24)
1973	24.22(.25)	24.40(.39)	22.52(.20)	19.54(.31)	19.16(.37)	17.36(.35)
1974	20.72(.30)	22.00(.36)	22.10(.31)	21.35(.36)	21.36(.24)	19.51(.19)
1975	21.25(.28)	22.41(.24)	23.41(.19)	22.21(.27)	20.81(.21)	18.67(.18)
1976	21.16(.30)	23.38(.64)	22.96(.33)	22.45(.35)	21.64(.28)	21.23(.30)
1977	23.69(.22)	23.46(.19)	22.44(.32)	20.44(.28)	19.77(.24)	19.66(.27)
1978	21.06(.24)	23.46(.25)	22.57(.25)	22.69(.32)	20.07(.34)	19.95(.49)
1979	22.42(.19)	23.11(.28)	23.62(.22)	22.71(.26)	20.37(.31)	20.61(.45)
1980	21.69(.25)	23.22(.21)	24.21(.21)	22.48(.29)	21.81(.17)	20.84(.13)
1981	20.90(.26)	22.80(.22)	22.10(.24)	20.99(.28)	20.73(.20)	19.44(.16)
1982	21.33(.22)	22.62(.30)	21.65(.23)	21.20(.24)	21.01(.22)	21.15(.41)
1983	26.42(.19)	27.38(.19)	27.99(.14)	27.93(.20)	27.72(.15)	25.93(.30)
1984	22.13(.22)	22.78(.29)	21.92(.26)	20.95(.33)	19.17(.31)	19.49(.28)

	Jul	Aug	Sep	Oct	Nov	Dec
1953	19.78(.27)	19.06(.21)	18.20(.34)	18.24(.35)	18.72(.40)	18.81(.41)
1954	14.60(.35)	15.57(.41)	14.91(.31)	14.22(.29)	17.11(.26)	19.24(.54)
1955	17.68(.53)	15.54(.45)	15.71(.28)	14.69(.37)	17.09(.24)	18.12(.37)
1956	18.94(.24)	17.65(.37)	17.48(.29)	16.75(.19)	18.38(.29)	19.23(.40)
1957	22.43(.34)	19.28(.34)	18.94(.19)	19.23(.17)	19.07(.16)	20.75(.16)
1958	19.63(.26)	17.37(.10)	17.80(.15)	17.90(.13)	18.98(.18)	20.25(.31)
1959	17.55(.15)	16.80(.12)	16.64(.18)	17.77(.20)	19.04(.20)	19.35(.15)
1960	17.65(.10)	17.42(.12)	17.17(.11)	17.53(.18)	18.78(.24)	20.59(.17)
1961	18.04(.22)	17.62(.11)	16.87(.11)	17.36(.16)	18.54(.14)	19.39(.17)
1962	17.30(.09)	17.27(.10)	16.77(.10)	16.89(.10)	18.08(.12)	19.49(.21)
1963	18.70(.13)	18.24(.17)	18.00(.11)	17.55(.16)	18.54(.28)	19.72(.17)
1964	17.10(.18)	16.11(.20)	16.11(.14)	16.40(.15)	18.31(.32)	19.76(.19)
1965	20.59(.20)	20.00(.20)	17.79(.16)	18.26(.23)	18.76(.13)	21.49(.15)
1966	18.00(.12)	16.75(.13)	16.81(.10)	17.37(.12)	18.13(.17)	19.77(.20)
1967	17.40(.16)	16.46(.17)	15.76(.13)	16.09(.21)	16.90(.18)	18.22(.21)
1968	17.64(.23)	17.05(.17)	18.26(.38)	17.65(.17)	17.67(.16)	20.82(.24)
1969	18.44(.20)	18.01(.17)	17.36(.19)	18.24(.16)	18.39(.13)	19.49(.15)
1970	15.72(.12)	16.19(.13)	16.33(.28)	16.36(.25)	17.94(.16)	18.29(.21)
1971	18.00(.28)	17.27(.23)	16.32(.26)	17.05(.27)	18.34(.15)	19.81(.35)
1972	21.18(.36)	21.77(.23)	19.29(.36)	19.17(.25)	20.61(.32)	21.73(.31)
1973	16.88(.32)	16.04(.16)	15.80(.22)	16.11(.31)	17.27(.24)	19.01(.30)
1974	18.12(.15)	17.48(.15)	16.70(.31)	16.91(.32)	18.96(.23)	19.83(.35)
1975	18.46(.25)	17.68(.36)	15.71(.24)	15.59(.20)	16.24(.15)	18.74(.24)
1976	21.18(.20)	19.51(.55)	19.00(.23)	19.19(.25)	20.04(.23)	21.46(.15)
1977	18.54(.25)	17.23(.22)	17.21(.28)	18.49(.28)	18.95(.16)	19.45(.24)
1978	18.49(.35)	16.91(.33)	17.27(.25)	18.11(.25)	19.40(.30)	20.49(.24)
1979	18.73(.25)	18.30(.26)	19.01(.28)	18.53(.23)	19.25(.27)	21.04(.38)
1980	20.04(.11)	18.35(.13)	17.77(.15)	18.39(.23)	18.95(.27)	20.21(.21)
1981	18.08(.17)	18.24(.11)	17.67(.24)	17.86(.23)	18.98(.15)	20.29(.15)
1982	19.65(.18)	18.34(.23)	19.00(.36)	20.61(.22)	23.03(.17)	25.19(.21)
1983	23.24(.23)	21.26(.21)	19.57(.25)	19.89(.14)	20.25(.22)	21.54(.27)
1984	19.52(.23)	18.37(.13)	18.44(.18)	18.27(.28)	19.70(.31)	20.20(.31)

Table 3. Total cloud amount. Values indicate mean fraction of sky obscured. The standard error of the mean appears in parentheses to the right of each mean value.

	Jan	Feb	Mar	Apr	May	Jun
1953	.66(.06)	.58(.06)	.43(.06)	.43(.08)	.54(.06)	.76(.10)
1954	.59(.05)	.75(.05)	.69(.07)	.35(.04)	.85(.05)	.74(.07)
1955	.55(.07)	.61(.06)	.60(.09)	.06(.04)	.69(.08)	.90(.04)
1956	.66(.05)	.46(.10)	.40(.06)	.53(.06)	.65(.08)	.89(.06)
1957	.48(.07)	.80(.05)	.56(.03)	.57(.05)	.55(.06)	.76(.04)
1958	.60(.03)	.68(.03)	.63(.03)	.32(.04)	.54(.04)	.83(.03)
1959	.40(.03)	.58(.02)	.66(.02)	.60(.03)	.83(.03)	.78(.04)
1960	.50(.03)	.50(.03)	.38(.02)	.44(.03)	.51(.03)	.63(.05)
1961	.65(.03)	.44(.03)	.65(.03)	.50(.03)	.49(.04)	.79(.03)
1962	.55(.02)	.54(.03)	.48(.03)	.56(.03)	.53(.04)	.79(.03)
1963	.50(.04)	.52(.03)	.61(.02)	.52(.03)	.66(.03)	.81(.02)
1964	.64(.03)	.66(.03)	.57(.04)	.51(.04)	.72(.06)	.63(.06)
1965	.54(.04)	.49(.04)	.61(.02)	.60(.03)	.63(.03)	.64(.03)
1966	.56(.03)	.44(.03)	.57(.03)	.45(.03)	.62(.03)	.76(.03)
1967	.72(.03)	.51(.05)	.56(.03)	.51(.03)	.46(.04)	.82(.04)
1968	.52(.04)	.52(.03)	.45(.03)	.38(.03)	.65(.04)	.75(.03)
1969	.57(.04)	.55(.04)	.58(.03)	.57(.04)	.70(.05)	.81(.03)
1970	.59(.04)	.43(.04)	.37(.03)	.43(.05)	.62(.04)	.81(.02)
1971	.51(.03)	.58(.04)	.48(.03)	.52(.05)	.68(.06)	.85(.06)
1972	.53(.04)	.49(.04)	.64(.03)	.53(.04)	.69(.04)	.78(.04)
1973	.67(.03)	.61(.05)	.60(.04)	.49(.04)	.40(.05)	.70(.05)
1974	.59(.03)	.52(.04)	.53(.03)	.53(.05)	.77(.03)	.89(.02)
1975	.69(.04)	.50(.04)	.60(.02)	.54(.03)	.72(.03)	.86(.03)
1976	.61(.04)	.59(.08)	.63(.03)	.55(.05)	.62(.04)	.87(.04)
1977	.54(.05)	.68(.03)	.55(.04)	.34(.03)	.53(.04)	.71(.04)
1978	.53(.04)	.65(.04)	.45(.04)	.57(.04)	.54(.05)	.68(.07)
1979	.50(.03)	.53(.04)	.56(.03)	.44(.03)	.67(.04)	.79(.05)
1980	.57(.03)	.53(.03)	.58(.03)	.48(.04)	.57(.03)	.80(.02)
1981	.66(.03)	.63(.03)	.51(.03)	.57(.03)	.66(.03)	.80(.03)
1982	.60(.03)	.58(.03)	.55(.03)	.52(.03)	.58(.04)	.84(.04)
1983	.52(.04)	.47(.02)	.63(.03)	.70(.03)	.75(.03)	.74(.04)
1984	.42(.04)	.43(.03)	.45(.03)	.40(.04)	.34(.05)	.74(.04)
	Jul	Aug	Sep	Oct	Nov	Dec
1953	.65(.14)	.91(.04)	.74(.07)	.74(.07)	.81(.06)	.67(.07)
1954	.79(.05)	.88(.07)	.92(.05)	.89(.04)	.72(.05)	.75(.08)
1955	.97(.02)	.90(.04)	.90(.04)	.80(.05)	.61(.08)	.44(.10)
1956	.85(.05)	.82(.08)	.84(.05)	.82(.05)	.73(.05)	.49(.08)
1957	.79(.06)	.72(.08)	.85(.04)	.72(.03)	.72(.03)	.64(.03)
1958	.79(.05)	.80(.03)	.90(.02)	.81(.03)	.52(.04)	.45(.06)
1959	.78(.03)	.78(.03)	.79(.04)	.79(.03)	.63(.04)	.51(.03)
1960	.72(.03)	.81(.03)	.90(.02)	.89(.03)	.63(.05)	.67(.04)
1961	.94(.01)	.83(.02)	.90(.02)	.78(.03)	.61(.02)	.60(.03)
1962	.90(.02)	.93(.02)	.86(.03)	.88(.02)	.77(.02)	.46(.04)
1963	.80(.03)	.80(.04)	.88(.02)	.82(.04)	.77(.04)	.68(.05)
1964	.87(.03)	.87(.03)	.86(.03)	.88(.02)	.77(.04)	.51(.03)
1965	.88(.03)	.90(.02)	.92(.02)	.86(.03)	.75(.02)	.61(.03)
1966	.77(.03)	.83(.03)	.85(.02)	.89(.02)	.83(.03)	.61(.03)
1967	.88(.03)	.91(.03)	.84(.03)	.85(.04)	.86(.03)	.47(.04)
1968	.80(.05)	.93(.02)	.88(.03)	.83(.03)	.76(.03)	.50(.04)
1969	.86(.04)	.83(.03)	.91(.02)	.82(.03)	.68(.03)	.56(.04)
1970	.87(.04)	.91(.03)	.85(.03)	.95(.02)	.59(.03)	.64(.04)
1971	.94(.02)	.88(.03)	.91(.03)	.85(.05)	.65(.04)	.65(.06)
1972	.83(.05)	.80(.04)	.87(.04)	.78(.04)	.86(.05)	.67(.05)
1973	.82(.03)	.91(.02)	.87(.03)	.80(.04)	.81(.03)	.72(.04)
1974	.91(.02)	.89(.03)	.88(.03)	.75(.05)	.72(.04)	.57(.05)
1975	.86(.03)	.89(.03)	.89(.03)	.77(.04)	.78(.04)	.64(.04)
1976	.80(.04)	.93(.03)	.77(.03)	.81(.03)	.78(.04)	.53(.04)
1977	.89(.03)	.86(.04)	.83(.04)	.81(.03)	.72(.02)	.41(.05)
1978	.95(.01)	.84(.04)	.80(.04)	.81(.04)	.68(.04)	.50(.03)
1979	.85(.03)	.81(.03)	.83(.03)	.81(.03)	.80(.03)	.49(.06)
1980	.90(.01)	.90(.02)	.81(.02)	.82(.02)	.69(.04)	.48(.04)
1981	.87(.02)	.83(.02)	.92(.02)	.67(.03)	.63(.03)	.51(.03)
1982	.80(.04)	.88(.03)	.82(.03)	.76(.03)	.75(.03)	.58(.03)
1983	.72(.03)	.68(.03)	.66(.06)	.80(.02)	.58(.04)	.49(.04)
1984	.81(.03)	.75(.03)	.86(.03)	.91(.03)	.70(.05)	.52(.04)

Table 4. Atmospheric pressure at sea level. Add 1000.0 to the mean values in the table to yield pressure in millibars. The standard error of the mean appears in parentheses to the right of each mean value; the standard errors are given (directly) in millibars.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	11.2(.3)	10.4(.1)	11.1(.3)	13.2(.5)	12.5(.2)	14.5(.5)	13.7(.5)	13.4(.2)	13.0(.2)	15.0(.5)	14.0(.3)	13.2(.4)
1954	12.3(.2)	12.2(.4)	10.2(.4)	11.3(.3)	13.5(.3)	14.7(.3)	13.8(.3)	14.3(.4)	13.8(.3)	14.8(.2)	14.5(.2)	13.0(.3)
1955	12.5(.3)	10.9(.2)	10.4(.4)	11.9(.5)	13.6(.2)	15.2(.2)	15.7(.3)	15.1(.3)	15.4(.3)	16.1(.3)	14.0(.2)	13.1(.5)
1956	11.5(.2)	10.7(.4)	11.1(.3)	10.9(.3)	12.0(.2)	10.0(.6)	14.9(.3)	13.7(.4)	14.4(.3)	14.1(.2)	14.2(.5)	9.4(.6)
1957	12.8(.2)	8.6(.3)	10.9(.3)	9.9(.3)	12.3(.2)	12.3(.2)	13.0(.3)	14.0(.3)	12.5(.3)	13.4(.2)	12.8(.2)	12.2(.2)
1958	11.9(.2)	11.5(.2)	7.2(.4)	9.8(.3)	11.5(.2)	13.2(.1)	14.1(.3)	13.8(.2)	14.0(.3)	12.7(.2)	12.8(.2)	10.6(1.7)
1959	12.0(.2)	10.9(.1)	11.5(.2)	11.2(.1)	13.3(.2)	14.2(.2)	13.6(.1)	14.1(.2)	13.1(.2)	13.7(.2)	13.3(.2)	12.2(.3)
1960	11.6(.2)	11.5(.2)	11.3(.2)	11.5(.1)	12.7(.1)	13.7(.2)	14.5(.1)	14.5(.2)	14.1(.1)	14.0(.2)	13.1(.2)	13.5(.3)
1961	10.6(.4)	10.6(.2)	10.6(.2)	11.2(.4)	12.9(.1)	13.6(.2)	14.4(.2)	14.4(.1)	14.7(.1)	13.5(.1)	14.7(.2)	13.2(.1)
1962	13.0(.1)	11.8(.2)	12.0(.1)	12.8(.2)	14.0(.2)	15.3(.1)	14.4(.1)	15.2(.2)	13.9(.3)	15.3(.2)	10.6(1.4)	13.8(.2)
1963	12.9(.2)	13.6(.2)	11.2(.1)	13.5(.4)	13.2(.1)	14.2(.1)	14.3(.2)	13.6(.3)	13.8(.4)	14.4(.1)	15.4(.4)	12.4(.2)
1964	12.3(.1)	10.5(.1)	11.2(.2)	12.2(.2)	12.7(.4)	14.2(.2)	14.8(.1)	14.8(.2)	14.2(.2)	14.3(.2)	13.1(.2)	13.2(.1)
1965	11.7(.1)	10.2(.2)	11.0(.2)	11.5(.1)	11.3(.2)	12.9(.2)	12.6(.2)	14.0(.2)	14.1(.2)	13.9(.2)	12.1(.2)	11.6(.1)
1966	10.6(.2)	10.2(.2)	10.2(.1)	11.8(.2)	13.2(.1)	14.6(.1)	14.0(.1)	14.9(.1)	14.8(.1)	14.1(.2)	13.6(.2)	12.3(.1)
1967	11.5(.2)	12.3(.2)	12.0(.2)	11.3(.2)	13.1(.2)	14.3(.2)	14.2(.2)	14.5(.2)	15.2(.2)	14.0(.2)	13.4(.2)	13.0(.2)
1968	11.3(.2)	11.7(.1)	12.6(.2)	12.9(.1)	14.3(.2)	15.6(.1)	14.8(.2)	15.2(.1)	14.0(.3)	13.5(.2)	14.1(.1)	12.6(.2)
1969	11.2(.3)	9.6(.1)	11.4(.2)	11.3(.1)	11.5(.2)	13.5(.2)	14.3(.2)	14.9(.2)	13.0(.1)	13.8(.1)	13.2(.2)	12.2(.1)
1970	12.8(.2)	11.0(.2)	11.8(.1)	11.7(.2)	14.5(.2)	14.4(.1)	15.5(.1)	14.4(.2)	13.8(.2)	13.9(.3)	13.9(.1)	11.0(.2)
1971	11.9(.2)	10.8(.2)	10.8(.2)	12.3(.2)	13.8(.3)	15.3(.4)	13.7(.3)	14.3(.7)	14.5(.4)	15.3(.2)	14.0(.1)	12.3(.3)
1972	10.9(.2)	11.0(.3)	10.3(.2)	11.5(.2)	11.8(.2)	12.1(.2)	12.5(.6)	12.8(.3)	12.9(.3)	13.1(.2)	12.2(.3)	11.8(.6)
1973	10.5(.4)	11.8(.2)	10.7(.2)	11.5(.3)	13.0(.3)	14.5(.2)	14.7(.4)	14.8(.2)	15.2(.3)	15.1(.2)	14.3(.2)	14.8(.2)
1974	11.9(.5)	11.8(.2)	12.5(.2)	12.6(.3)	13.7(.3)	14.2(.2)	13.8(.4)	14.7(.2)	14.9(.2)	14.0(.2)	13.7(.1)	12.6(.2)
1975	11.5(.3)	11.9(.2)	11.4(.1)	11.9(.2)	13.5(.1)	14.0(.1)	15.2(.2)	15.1(.3)	15.5(.2)	15.3(.2)	15.1(.2)	13.5(.2)
1976	12.1(.3)	11.6(.7)	10.6(.1)	11.9(.2)	12.5(.2)	12.0(.2)	13.3(.2)	14.6(.6)	13.3(.4)	13.7(.3)	13.9(.2)	10.4(.2)
1977	10.4(.3)	11.2(.1)	10.0(.2)	12.0(.4)	12.6(.2)	13.7(.2)	13.5(.3)	14.3(.2)	14.7(.2)	14.2(.2)	13.7(.2)	12.4(.2)
1978	13.9(.3)	10.1(.7)	12.0(.2)	12.3(.2)	12.8(.2)	15.0(.3)	13.9(.4)	14.1(.2)	14.5(.2)	13.8(.2)	12.3(.2)	12.3(.2)
1979	12.2(.1)	11.9(.3)	11.4(.2)	11.0(.3)	13.3(.3)	15.5(.5)	14.9(.2)	14.2(.3)	14.7(.3)	14.8(.2)	14.1(.3)	12.5(.9)
1980	11.9(.2)	12.3(.2)	9.3(.2)	10.5(.2)	12.9(.2)	14.5(.3)	15.1(.2)	15.2(.2)	14.1(.4)	13.8(.3)	13.8(.2)	13.7(.5)
1981	13.9(.3)	10.8(.2)	11.4(.2)	12.1(.2)	14.3(.2)	13.8(.4)	15.0(.3)	16.0(.2)	14.8(.2)	13.9(.2)	13.4(.2)	11.9(.1)
1982	12.6(.5)	11.4(.2)	10.4(.2)	12.1(.2)	12.6(.2)	12.9(.3)	12.0(.2)	12.9(.2)	14.1(.3)	12.9(.2)	10.6(.2)	10.0(.2)
1983	9.1(.3)	9.7(.2)	9.1(.2)	9.5(.2)	9.6(.3)	11.6(.2)	11.8(.2)	14.2(.4)	15.0(.5)	13.6(.2)	13.3(.7)	14.2(.4)
1984	12.5(.2)	10.7(.3)	10.7(.5)	13.1(.3)	13.7(.7)	13.9(.2)	12.6(.4)	15.3(.3)	14.8(.5)	14.5(.3)	14.2(.1)	11.8(.3)

Table 5. Alongshore component (positive equatorward) of wind stress on the sea surface. Units are dynes per square centimeter. The standard error of the mean appears in parentheses to the right of the mean alongshore stress value. Values in this table multiplied by the factor 3.95 (see text) yield offshore Ekman transport in cubic meters per second across each meter width.

	Jan	*Feb*	*Mar*	*Apr*	*May*	*Jun*
1953	.36(.06)	.32(.05)	.44(.07)	.99(.20)	.83(.09)	.37(.10)
1954	.24(.03)	.41(.14)	.10(.02)	.46(.05)	.56(.08)	.46(.08)
1955	.40(.09)	.16(.03)	.53(.18)	.18(.08)	.63(.11)	.45(.09)
1956	.16(.02)	.25(.07)	.67(.10)	.83(.09)	.85(.13)	.50(.05)
1957	.31(.06)	.53(.11)	.76(.05)	.86(.10)	.57(.06)	.76(.07)
1958	.40(.05)	.42(.05)	.45(.05)	.61(.06)	.57(.07)	.46(.04)
1959	.34(.03)	.28(.02)	.40(.03)	.42(.04)	.30(.03)	.59(.07)
1960	.23(.03)	.27(.02)	.41(.03)	.49(.04)	.53(.09)	.45(.04)
1961	.20(.02)	.27(.03)	.39(.04)	.48(.03)	.70(.06)	.48(.05)
1962	.42(.02)	.34(.03)	.47(.03)	.52(.04)	.51(.04)	.60(.04)
1963	.32(.04)	.39(.03)	.61(.03)	.47(.03)	.59(.04)	.33(.03)
1964	.49(.04)	.44(.03)	.51(.05)	.71(.07)	.63(.07)	.58(.12)
1965	.29(.04)	.40(.05)	.40(.03)	.53(.06)	.97(.07)	.58(.04)
1966	.60(.04)	.61(.06)	.46(.04)	.75(.06)	.59(.05)	.62(.04)
1967	.40(.04)	.36(.04)	.29(.03)	.30(.03)	.37(.04)	.71(.10)
1968	.15(.02)	.40(.05)	.36(.03)	.36(.03)	.34(.05)	.65(.05)
1969	.29(.04)	.26(.04)	.47(.04)	.56(.04)	.45(.07)	.89(.08)
1970	.33(.04)	.16(.05)	.40(.05)	.56(.06)	.55(.05)	.52(.04)
1971	.17(.04)	.36(.04)	.34(.03)	.59(.08)	.43(.07)	.73(.23)
1972	.29(.03)	.34(.04)	.56(.11)	.55(.04)	.42(.04)	.67(.08)
1973	.57(.06)	.38(.05)	.73(.05)	.68(.08)	.67(.11)	.51(.07)
1974	.32(.04)	.42(.05)	.48(.04)	.68(.07)	.71(.05)	.66(.07)
1975	.40(.04)	.35(.04)	.72(.05)	.63(.05)	.74(.04)	.63(.06)
1976	.21(.04)	.17(.04)	.51(.05)	.77(.07)	.72(.07)	.56(.08)
1977	.32(.06)	.56(.06)	.38(.04)	.57(.05)	.47(.05)	.67(.05)
1978	.37(.05)	.47(.06)	.62(.07)	.71(.08)	.59(.07)	.72(.12)
1979	.49(.05)	.54(.09)	.54(.04)	.68(.05)	.69(.07)	.92(.14)
1980	.44(.04)	.47(.05)	.49(.04)	.49(.05)	.89(.07)	.58(.03)
1981	.52(.04)	.30(.03)	.46(.04)	.54(.04)	.53(.05)	.84(.08)
1982	.35(.04)	.47(.04)	.63(.04)	.55(.04)	.65(.06)	.91(.12)
1983	.69(.06)	.66(.04)	.46(.05)	.74(.08)	.75(.06)	1.07(.09)
1984	.26(.04)	.53(.11)	.80(.13)	.31(.11)	.83(.18)	.87(.13)

	Jul	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*
1953	.70(.22)	.36(.05)	.46(.06)	.53(.08)	.62(.08)	.27(.05)
1954	.52(.07)	.89(.21)	.83(.09)	.24(.02)	.30(.04)	.20(.04)
1955	.46(.09)	.88(.14)	.66(.10)	.65(.12)	.60(.08)	.11(.04)
1956	.69(.09)	.52(.13)	.64(.05)	.50(.08)	.45(.04)	.45(.08)
1957	1.01(.11)	.54(.08)	.75(.07)	.56(.06)	.44(.04)	.56(.04)
1958	.51(.05)	.71(.06)	.49(.04)	.43(.04)	.26(.03)	.39(.05)
1959	.38(.04)	.53(.04)	.48(.07)	.44(.05)	.31(.03)	.23(.03)
1960	.59(.05)	.55(.04)	.51(.04)	.48(.06)	.34(.03)	.36(.04)
1961	.67(.06)	.50(.04)	.50(.04)	.40(.03)	.38(.02)	.31(.03)
1962	.60(.04)	.49(.04)	.60(.06)	.49(.04)	.51(.04)	.23(.02)
1963	.54(.05)	.48(.06)	.72(.05)	.72(.11)	.53(.06)	.36(.04)
1964	.62(.05)	.71(.09)	.73(.08)	.57(.04)	.36(.05)	.42(.04)
1965	.63(.05)	.84(.07)	.87(.07)	.60(.07)	.49(.03)	.49(.04)
1966	.76(.04)	.74(.06)	.59(.03)	.52(.04)	.26(.03)	.26(.02)
1967	.54(.05)	.72(.07)	.74(.09)	.73(.09)	.46(.05)	.55(.06)
1968	.90(.10)	.72(.08)	.64(.08)	.59(.03)	.51(.03)	.62(.08)
1969	.58(.06)	.71(.08)	.59(.05)	.42(.04)	.28(.03)	.37(.04)
1970	.57(.06)	.52(.05)	.45(.04)	.50(.07)	.41(.03)	.27(.05)
1971	.46(.08)	.77(.11)	.64(.12)	.71(.08)	.43(.05)	.49(.09)
1972	.90(.11)	.81(.10)	1.32(.19)	.49(.05)	.35(.04)	.72(.15)
1973	.70(.11)	1.16(.12)	1.01(.11)	.71(.09)	.58(.05)	.37(.06)
1974	.73(.05)	.64(.08)	.72(.07)	.67(.07)	.68(.05)	.45(.06)
1975	.64(.07)	.91(.10)	.73(.05)	.51(.05)	.36(.04)	.35(.05)
1976	.59(.05)	.69(.16)	.80(.06)	.67(.06)	.64(.06)	.52(.06)
1977	.94(.11)	.83(.10)	.47(.06)	.46(.04)	.57(.04)	.55(.06)
1978	.87(.14)	.69(.08)	.73(.09)	.54(.06)	.51(.06)	.47(.05)
1979	.65(.07)	.66(.09)	.71(.07)	.65(.05)	.54(.05)	.46(.07)
1980	1.01(.04)	.74(.04)	.75(.06)	.65(.05)	.47(.04)	.49(.06)
1981	.77(.07)	.64(.04)	.85(.09)	.41(.04)	.57(.04)	.42(.03)
1982	.89(.08)	.63(.06)	.96(.12)	.84(.06)	.73(.04)	.66(.05)
1983	.86(.06)	.69(.06)	.77(.07)	.60(.05)	.38(.10)	.23(.05)
1984	.61(.06)	.76(.06)	.64(.07)	.60(.04)	.86(.06)	.58(.05)

Table 6. Onshore component of wind stress on the sea surface. Units are dynes per square centimeter. The standard error of the mean appears in parentheses to the right of each mean onshore stress value.

	Jan	*Feb*	*Mar*	*Apr*	*May*	*Jun*
1953	.10(.03)	.02(.03)	.00(.05)	-.12(.04)	.02(.04)	-.06(.05)
1954	.04(.01)	.07(.05)	.00(.01)	.10(.02)	-.04(.03)	.04(.02)
1955	-.04(.03)	.02(.01)	.19(.07)	.09(.08)	-.01(.03)	-.01(.03)
1956	.06(.03)	.08(.03)	.08(.08)	.01(.04)	.01(.05)	.10(.04)
1957	.05(.02)	-.06(.05)	-.06(.02)	-.04(.03)	.00(.04)	.06(.03)
1958	.07(.01)	.08(.02)	.09(.02)	.01(.02)	.02(.02)	.08(.02)
1959	.05(.01)	.07(.01)	.01(.02)	.06(.01)	.04(.02)	.17(.03)
1960	.07(.01)	.04(.01)	.05(.01)	.04(.02)	.03(.01)	.02(.02)
1961	.03(.01)	.01(.01)	.06(.02)	.05(.01)	.03(.02)	.04(.02)
1962	.08(.01)	.01(.02)	.04(.01)	.02(.02)	.02(.02)	-.03(.01)
1963	.06(.01)	.02(.02)	.08(.01)	.01(.01)	.01(.02)	.01(.01)
1964	.05(.02)	.03(.01)	.04(.02)	-.07(.03)	.00(.04)	.06(.03)
1965	.06(.02)	.05(.02)	.01(.01)	.06(.02)	-.08(.03)	.03(.02)
1966	.05(.02)	.06(.02)	.09(.03)	-.06(.02)	.03(.02)	.06(.02)
1967	.02(.02)	.08(.02)	.02(.02)	.03(.01)	.09(.02)	.08(.05)
1968	.03(.01)	.02(.02)	.04(.01)	.02(.01)	.01(.03)	.01(.02)
1969	.04(.01)	.04(.02)	.00(.01)	.03(.02)	.05(.03)	-.03(.03)
1970	.04(.02)	-.08(.05)	.05(.02)	.10(.03)	.08(.02)	.03(.01)
1971	.05(.02)	.04(.02)	.00(.02)	.03(.04)	-.03(.02)	-.08(.07)
1972	.04(.01)	-.06(.05)	-.06(.07)	.03(.02)	.00(.02)	.06(.04)
1973	.13(.03)	.07(.02)	-.02(.02)	.13(.04)	-.02(.04)	.15(.05)
1974	.04(.02)	.02(.02)	-.04(.02)	.02(.04)	-.01(.02)	.03(.03)
1975	.02(.02)	.07(.02)	-.05(.02)	-.04(.02)	.00(.02)	-.01(.02)
1976	.03(.01)	.02(.04)	.01(.02)	-.06(.04)	.01(.02)	.03(.04)
1977	.07(.02)	-.03(.03)	.06(.02)	.07(.03)	.02(.02)	-.01(.03)
1978	.04(.03)	.09(.03)	.05(.03)	-.03(.02)	.03(.02)	-.07(.05)
1979	.03(.02)	-.08(.04)	.08(.03)	.03(.02)	-.03(.03)	-.04(.04)
1980	.08(.02)	.06(.02)	.02(.02)	.03(.03)	-.05(.03)	-.08(.02)
1981	.02(.02)	.00(.02)	.05(.02)	-.01(.02)	.01(.02)	.01(.03)
1982	.06(.02)	.10(.03)	.00(.02)	-.01(.02)	.06(.03)	-.09(.06)
1983	.15(.03)	.00(.02)	-.03(.03)	-.01(.07)	.07(.03)	.05(.04)
1984	.06(.02)	-.04(.02)	-.08(.06)	-.10(.06)	.08(.07)	.14(.05)
	Jul	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*
1953	.15(.04)	.06(.02)	.12(.03)	.07(.07)	.08(.03)	.04(.02)
1954	.06(.03)	-.02(.11)	.19(.08)	.04(.01)	.21(.05)	.08(.02)
1955	.08(.04)	.04(.06)	.09(.04)	.09(.02)	.12(.05)	.05(.01)
1956	.02(.06)	.31(.08)	.13(.04)	.14(.03)	.06(.03)	.06(.02)
1957	-.05(.09)	.18(.05)	.05(.03)	.07(.02)	.10(.02)	.11(.02)
1958	.12(.03)	.23(.05)	.12(.02)	.20(.03)	.05(.01)	.06(.02)
1959	.04(.02)	.12(.02)	.17(.06)	.05(.01)	.05(.01)	.04(.01)
1960	.06(.02)	.07(.02)	.06(.02)	.07(.02)	.02(.01)	.06(.02)
1961	.04(.02)	.03(.01)	.08(.02)	.15(.03)	.03(.01)	.04(.01)
1962	.05(.01)	.12(.02)	.10(.02)	.08(.02)	.08(.01)	.09(.02)
1963	.03(.02)	.01(.02)	.09(.02)	.05(.03)	.03(.04)	.07(.02)
1964	.04(.02)	.05(.05)	.10(.03)	.11(.02)	.05(.02)	.04(.02)
1965	.01(.03)	-.02(.02)	.10(.03)	.17(.04)	.13(.03)	.08(.02)
1966	.05(.02)	.15(.03)	.08(.02)	.15(.02)	.06(.01)	.02(.01)
1967	.08(.02)	.06(.04)	-.01(.03)	.09(.03)	.03(.02)	.12(.03)
1968	.03(.04)	.09(.03)	.12(.05)	.11(.02)	.08(.01)	-.06(.04)
1969	.02(.02)	-.02(.02)	.08(.02)	.04(.01)	.07(.01)	.09(.02)
1970	.07(.02)	.08(.02)	.10(.02)	.18(.04)	.12(.03)	.09(.03)
1971	.01(.03)	.14(.04)	-.01(.03)	.00(.03)	.06(.02)	-.02(.04)
1972	.04(.04)	.07(.03)	.12(.08)	.10(.03)	.19(.04)	.14(.03)
1973	-.03(.04)	.01(.05)	.01(.06)	.01(.05)	.01(.02)	.06(.03)
1974	.02(.02)	.04(.03)	.13(.03)	.12(.03)	.03(.03)	.13(.03)
1975	.06(.03)	.03(.05)	.06(.03)	.11(.03)	.08(.03)	.04(.02)
1976	.03(.04)	-.01(.06)	.09(.03)	.15(.03)	.02(.04)	.13(.04)
1977	.05(.07)	-.10(.04)	.10(.03)	.08(.02)	.07(.01)	.02(.03)
1978	-.11(.05)	.04(.04)	.07(.03)	.08(.03)	.07(.02)	.05(.02)
1979	-.01(.03)	.10(.03)	-.02(.04)	.07(.02)	.08(.03)	.06(.06)
1980	-.12(.02)	-.02(.03)	.04(.03)	.05(.02)	.06(.02)	-.01(.02)
1981	-.04(.03)	-.05(.01)	.01(.03)	.07(.02)	.05(.02)	-.04(.01)
1982	.05(.04)	.04(.02)	.01(.06)	.15(.04)	.09(.02)	.08(.02)
1983	-.03(.02)	-.01(.03)	-.10(.03)	.02(.03)	.04(.03)	.04(.03)
1984	.07(.05)	-.12(.05)	.03(.04)	.02(.04)	-.09(.03)	-.01(.03)

Table 7. "Wind cubed" index of rate of addition to the water column, by the wind, of turbulent mixing energy. The standard errors of the mean appear in parentheses to the right of each mean index value. Nominal units are $m^3 sec^{-3}$.

	Jan	*Feb*	*Mar*	*Apr*	*May*	*Jun*
1953	130(34)	107(19)	162(35)	473(140)	354(44)	130(47)
1954	75(16)	205(85)	19(4)	186(32)	210(46)	174(41)
1955	132(40)	37(9)	316(101)	93(22)	238(67)	177(50)
1956	58(15)	91(30)	287(46)	355(51)	377(68)	182(25)
1957	101(22)	220(44)	310(23)	375(64)	201(27)	337(42)
1958	184(48)	171(32)	181(25)	260(37)	244(46)	192(21)
1959	116(13)	94(8)	143(14)	154(18)	104(16)	300(47)
1960	84(11)	86(10)	151(15)	207(18)	307(95)	161(19)
1961	71(9)	83(11)	173(24)	178(13)	301(37)	204(26)
1962	156(12)	127(16)	171(14)	220(24)	197(20)	226(19)
1963	113(19)	141(19)	252(17)	176(14)	230(20)	113(13)
1964	188(20)	156(14)	198(27)	295(36)	248(41)	315(117)
1965	100(17)	155(33)	144(16)	238(51)	467(45)	232(20)
1966	247(26)	263(30)	213(25)	312(35)	252(34)	263(24)
1967	147(16)	143(25)	94(13)	102(11)	140(20)	387(80)
1968	47(10)	172(30)	126(15)	120(11)	142(25)	272(25)
1969	97(16)	113(19)	174(18)	206(23)	193(34)	432(68)
1970	121(17)	148(36)	166(38)	232(35)	227(25)	218(20)
1971	92(16)	128(25)	120(15)	266(42)	155(30)	404(162)
1972	102(14)	146(33)	346(70)	214(25)	146(18)	315(51)
1973	247(29)	136(21)	292(26)	333(49)	314(75)	279(52)
1974	121(17)	155(24)	181(20)	308(62)	300(29)	295(39)
1975	135(18)	140(22)	308(24)	251(21)	304(24)	272(33)
1976	76(22)	68(19)	196(27)	326(39)	308(36)	248(53)
1977	134(44)	251(40)	158(21)	265(27)	191(27)	263(30)
1978	150(22)	214(33)	280(44)	316(54)	246(35)	327(91)
1979	202(33)	250(54)	241(23)	282(29)	331(38)	459(122)
1980	179(19)	212(32)	203(21)	194(23)	441(47)	241(18)
1981	205(22)	104(13)	195(19)	212(21)	226(27)	431(73)
1982	134(21)	199(20)	259(19)	201(20)	300(29)	491(97)
1983	319(31)	262(18)	203(21)	420(117)	373(35)	539(61)
1984	118(21)	307(120)	534(117)	2[illegible](110)	636(159)	522(116)

	Jul	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*
1953	332(129)	125(26)	179(34)	217(43)	243(50)	74(16)
1954	207(37)	445(135)	439(73)	64(8)	161(33)	59(13)
1955	179(41)	460(100)	308(76)	322(79)	266(42)	30(13)
1956	324(56)	346(65)	261(29)	237(56)	184(23)	158(35)
1957	484(66)	253(52)	331(45)	261(38)	189(24)	238(22)
1958	214(25)	474(56)	214(26)	228(30)	92(16)	152(26)
1959	138(16)	233(23)	303(76)	164(23)	108(15)	82(13)
1960	260(32)	222(25)	201(19)	198(35)	99(12)	144(24)
1961	290(39)	191(17)	211(20)	199(24)	136(12)	100(12)
1962	265(22)	236(23)	267(32)	199(20)	212(19)	96(15)
1963	220(26)	176(25)	320(31)	376(72)	222(33)	131(19)
1964	250(25)	385(89)	372(58)	242(22)	132(20)	164(21)
1965	263(29)	392(45)	442(52)	319(44)	240(21)	193(20)
1966	317(29)	388(39)	245(18)	243(28)	95(12)	83(10)
1967	222(28)	336(41)	357(59)	369(57)	180(30)	280(45)
1968	442(61)	352(56)	326(62)	243(19)	192(16)	283(42)
1969	237(33)	312(52)	272(29)	154(26)	104(13)	151(23)
1970	248(34)	212(28)	186(22)	251(50)	194(24)	139(22)
1971	190(49)	425(71)	258(66)	302(49)	169(23)	199(57)
1972	423(63)	400(67)	805(139)	220(27)	156(25)	407(157)
1973	369(81)	784(81)	675(74)	348(66)	237(28)	179(37)
1974	299(28)	317(57)	352(45)	295(42)	274(28)	195(31)
1975	284(35)	461(58)	316(31)	235(35)	143(24)	147(23)
1976	264(36)	377(87)	370(33)	328(37)	270(49)	235(43)
1977	529(95)	392(59)	229(37)	189(21)	241(17)	220(34)
1978	434(85)	310(54)	350(82)	226(29)	237(49)	203(28)
1979	290(51)	433(73)	350(51)	274(33)	233(28)	226(50)
1980	458(27)	354(31)	382(35)	271(28)	181(22)	188(30)
1981	420(49)	244(21)	457(60)	166(18)	249(22)	146(13)
1982	438(52)	270(40)	549(82)	454(57)	316(22)	275(30)
1983	379(34)	330(39)	318(43)	277(33)	227(111)	122(32)
1984	334(58)	415(88)	328(46)	242(30)	350(27)	229(22)

Table 8. Daily total (both direct and diffuse) solar radiation absorbed by the ocean, Q_S. The standard error of the mean appears in parentheses to the right of each mean value. Units are watts/m^2. (Values may be converted to units of cal cm^{-2} day^{-1} by multiplying by the factor 2.064.)

	Jan	*Feb*	*Mar*	*Apr*	*May*	*Jun*
1953	239(12)	253(9)	262(11)	258(15)	193(9)	182(22)
1954	240(9)	214(10)	227(12)	241(6)	141(7)	158(11)
1955	250(12)	254(12)	236(17)	282(8)	182(17)	125(5)
1956	255(16)	269(16)	257(31)	230(12)	181(14)	121(3)
1957	264(12)	203(11)	243(7)	221(8)	190(10)	153(7)
1958	244(5)	236(8)	243(9)	248(9)	202(8)	148(6)
1959	287(7)	247(8)	241(9)	208(10)	169(12)	144(6)
1960	268(9)	269(4)	283(3)	236(4)	204(4)	167(7)
1961	242(5)	276(5)	228(5)	221(4)	205(6)	140(4)
1962	258(5)	257(4)	260(4)	214(4)	192(6)	143(3)
1963	263(6)	265(5)	240(4)	217(0)	176(4)	139(3)
1964	243(6)	236(4)	242(6)	223(6)	162(8)	161(7)
1965	257(8)	268(7)	236(4)	218(4)	183(4)	165(4)
1966	252(5)	279(5)	246(5)	236(4)	182(5)	148(4)
1967	218(5)	264(8)	244(5)	230(4)	207(6)	138(5)
1968	250(7)	263(5)	265(5)	244(4)	174(6)	149(4)
1969	248(7)	257(6)	238(4)	216(5)	168(7)	140(4)
1970	245(7)	274(7)	280(4)	236(7)	178(5)	140(2)
1971	264(6)	255(6)	261(5)	230(7)	169(8)	130(6)
1972	256(6)	271(7)	237(6)	221(5)	170(6)	145(6)
1973	236(7)	247(9)	237(5)	229(7)	216(7)	151(7)
1974	250(6)	268(7)	257(5)	219(8)	156(4)	131(3)
1975	234(7)	268(6)	240(4)	224(5)	163(4)	131(3)
1976	245(7)	248(13)	234(5)	218(8)	178(6)	130(5)
1977	259(8)	235(4)	244(6)	253(4)	187(5)	154(5)
1978	258(8)	240(7)	265(6)	217(6)	190(6)	153(9)
1979	270(5)	264(7)	246(5)	238(5)	171(5)	142(7)
1980	248(6)	261(5)	244(5)	231(7)	187(4)	156(5)
1981	233(5)	241(5)	249(5)	218(5)	183(6)	142(3)
1982	246(6)	257(5)	246(4)	230(5)	187(5)	139(6)
1983	260(8)	273(4)	236(5)	201(5)	163(4)	149(5)
1984	263(9)	268(7)	260(10)	223(10)	204(29)	142(6)

	Jul	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*
1953	170(20)	142(3)	204(12)	227(16)	211(13)	266(15)
1954	149(8)	144(5)	158(5)	192(7)	225(19)	184(11)
1955	123(2)	154(7)	159(2)	217(10)	241(15)	263(26)
1956	134(7)	157(11)	184(9)	198(10)	195(9)	261(31)
1957	143(11)	170(12)	186(8)	211(6)	216(8)	235(6)
1958	154(11)	165(5)	173(7)	218(9)	254(8)	278(13)
1959	154(6)	169(8)	190(8)	218(13)	226(7)	256(6)
1960	163(4)	171(6)	171(4)	185(5)	219(11)	235(7)
1961	126(2)	159(3)	170(2)	210(6)	243(4)	240(5)
1962	133(2)	148(2)	173(5)	193(4)	211(4)	258(6)
1963	145(4)	167(6)	177(4)	204(6)	212(6)	229(9)
1964	138(4)	154(5)	183(5)	191(3)	210(7)	257(6)
1965	135(4)	148(3)	169(3)	197(5)	219(4)	241(5)
1966	151(4)	162(4)	181(3)	191(3)	202(4)	241(5)
1967	137(4)	148(3)	184(5)	195(5)	196(5)	258(6)
1968	145(5)	145(3)	180(5)	201(4)	214(5)	256(7)
1969	137(5)	158(4)	165(3)	205(5)	226(5)	246(6)
1970	134(4)	152(4)	181(4)	180(3)	244(5)	235(7)
1971	127(2)	151(4)	171(7)	193(7)	236(6)	233(10)
1972	138(7)	161(6)	183(8)	209(6)	195(7)	229(9)
1973	142(4)	149(3)	174(5)	205(7)	208(5)	221(6)
1974	127(2)	154(4)	175(4)	218(8)	222(6)	250(8)
1975	134(4)	156(5)	173(4)	212(7)	211(7)	234(6)
1976	147(5)	143(6)	194(6)	206(6)	212(8)	257(8)
1977	134(4)	155(5)	187(6)	204(5)	223(4)	270(8)
1978	126(2)	160(5)	187(6)	205(7)	231(7)	264(6)
1979	138(4)	167(5)	179(5)	217(8)	210(6)	252(12)
1980	139(5)	158(4)	196(5)	208(5)	231(8)	266(9)
1981	139(4)	168(6)	169(2)	235(6)	241(4)	255(4)
1982	150(6)	151(4)	186(6)	215(5)	218(5)	253(6)
1983	156(5)	161(7)	184(12)	198(4)	258(12)	246(10)
1984	157(7)	165(6)	175(16)	185(6)	246(16)	242(9)

Table 9. Radiative heat loss, Q_B. The standard error of the mean appears in parentheses to the right of each mean value. Units are watts/m^2. (Values may be converted to units of cal cm^{-2} day^{-1} by multiplying by the factor 2.064.)

	Jan	*Feb*	*Mar*	*Apr*	*May*	*Jun*
1953	23(2)	28(2)	32(3)	41(5)	33(3)	33(10)
1954	26(2)	16(2)	22(3)	43(2)	16(3)	30(5)
1955	30(3)	27(3)	29(5)	60(5)	29(7)	10(2)
1956	33(5)	34(5)	38(13)	41(5)	28(5)	7(1)
1957	33(3)	13(2)	26(2)	29(2)	28(3)	21(2)
1958	24(1)	22(2)	27(2)	39(3)	36(2)	20(2)
1959	43(2)	24(2)	28(2)	29(3)	22(4)	18(2)
1960	32(2)	33(1)	44(1)	37(1)	38(1)	31(3)
1961	26(1)	34(1)	25(1)	34(1)	39(2)	19(1)
1962	31(1)	31(1)	36(1)	30(1)	35(2)	21(1)
1963	33(1)	31(1)	27(1)	34(0)	27(1)	18(1)
1964	27(1)	23(1)	30(1)	34(2)	23(3)	30(3)
1965	33(2)	34(2)	27(1)	27(1)	27(1)	28(1)
1966	30(1)	37(1)	29(1)	38(1)	29(1)	21(1)
1967	20(1)	33(2)	30(1)	34(1)	38(2)	19(2)
1968	33(2)	33(1)	36(1)	44(1)	28(2)	23(2)
1969	29(2)	30(1)	28(1)	29(1)	23(2)	18(1)
1970	29(2)	35(2)	42(1)	37(2)	29(2)	19(1)
1971	34(1)	30(1)	35(1)	34(2)	26(3)	15(2)
1972	32(1)	32(2)	24(1)	31(2)	24(2)	18(2)
1973	22(1)	24(2)	27(1)	36(2)	43(2)	25(3)
1974	30(1)	33(2)	33(1)	34(2)	20(1)	14(1)
1975	23(1)	32(1)	27(1)	32(1)	23(1)	15(1)
1976	27(1)	30(5)	25(1)	31(2)	29(2)	14(2)
1977	30(2)	22(1)	29(1)	43(1)	33(2)	25(2)
1978	31(2)	24(2)	34(1)	31(2)	33(2)	25(4)
1979	33(1)	30(1)	27(1)	36(1)	25(2)	20(3)
1980	30(1)	29(1)	28(1)	34(2)	31(1)	25(2)
1981	24(1)	24(1)	31(1)	31(1)	28(2)	18(1)
1982	29(1)	28(1)	0(1)	35(1)	32(2)	16(2)
1983	28(2)	31(1)	22(1)	20(1)	18(1)	19(2)
1984	29(2)	31(2)	32(3)	29(3)	37(10)	17(2)

	Jul	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*
1953	30(9)	9(1)	22(4)	26(5)	20(4)	34(3)
1954	20(3)	11(3)	10(2)	14(2)	23(5)	12(3)
1955	8(0)	14(3)	8(1)	22(3)	31(5)	39(10)
1956	16(3)	18(5)	15(3)	19(4)	15(3)	35(9)
1957	17(5)	19(4)	18(2)	21(2)	22(2)	25(1)
1958	22(4)	20(2)	14(2)	25(3)	35(2)	43(4)
1959	22(2)	19(3)	21(3)	24(5)	25(2)	34(1)
1960	27(1)	23(2)	15(1)	11(1)	23(3)	27(2)
1961	10(0)	17(1)	13(0)	20(2)	31(1)	29(1)
1962	14(0)	11(0)	15(1)	15(1)	20(1)	37(2)
1963	19(1)	19(2)	14(1)	18(2)	21(2)	26(2)
1964	15(1)	15(2)	16(1)	15(1)	20(2)	35(1)
1965	14(1)	13(1)	12(0)	15(1)	22(1)	29(1)
1966	22(1)	18(1)	16(1)	14(1)	17(1)	29(1)
1967	15(1)	13(1)	17(2)	16(2)	15(1)	39(2)
1968	20(3)	11(1)	14(1)	17(1)	22(1)	34(2)
1969	15(2)	17(1)	12(1)	18(1)	26(1)	31(1)
1970	15(2)	13(1)	16(1)	10(1)	32(1)	29(2)
1971	11(1)	13(1)	12(2)	17(3)	28(2)	26(3)
1972	15(2)	19(2)	15(2)	20(2)	15(2)	25(2)
1973	17(1)	12(1)	15(1)	20(2)	18(1)	23(1)
1974	13(1)	14(1)	15(1)	23(2)	23(2)	32(2)
1975	15(1)	14(2)	14(1)	23(2)	20(2)	28(2)
1976	19(2)	11(1)	20(1)	18(1)	19(2)	33(2)
1977	14(1)	16(2)	17(2)	19(1)	23(1)	41(2)
1978	9(0)	17(2)	19(2)	19(2)	25(2)	34(1)
1979	16(2)	19(2)	15(1)	22(2)	19(2)	32(4)
1980	13(1)	15(1)	20(1)	19(1)	27(2)	38(2)
1981	15(1)	19(2)	11(0)	29(2)	30(1)	35(1)
1982	19(2)	13(1)	17(2)	21(1)	20(1)	30(1)
1983	24(2)	17(2)	15(3)	15(1)	33(3)	28(3)
1984	21(2)	22(2)	18(8)	11(1)	29(5)	29(3)

Table 10. Evaporative heat loss, Q_c. The standard error of the mean appears in parentheses to the right of each mean value. Units are watts/m^2. (Values may be converted to units of cal $cm^{-2}day^{-1}$ by multiplying by the factor 2.064.)

	Jan	*Feb*	*Mar*	*Apr*	*May*	*Jun*
1953	3(6)	34(10)	39(8)	62(16)	97(11)	8(9)
1954	-23(5)	15(4)	8(3)	-24(4)	27(5)	33(4)
1955	22(7)	-26(5)	39(16)	14(10)	-14(12)	6(5)
1956	17(6)	-27(13)	-1(25)	39(11)	23(9)	33(6)
1957	-11(3)	43(9)	46(10)	68(13)	59(8)	64(11)
1958	22(4)	65(7)	31(8)	37(6)	49(11)	40(5)
1959	15(3)	15(4)	59(9)	42(7)	21(10)	35(6)
1960	11(2)	18(2)	32(4)	22(3)	15(1)	24(4)
1961	9(2)	22(2)	15(4)	18(2)	34(4)	36(4)
1962	22(2)	33(3)	16(3)	16(4)	26(3)	50(3)
1963	16(3)	24(2)	35(3)	31(0)	46(3)	31(2)
1964	25(3)	25(2)	19(3)	34(7)	28(5)	30(6)
1965	34(6)	46(5)	45(3)	57(5)	109(7)	62(3)
1966	36(4)	63(6)	30(4)	51(6)	44(4)	40(3)
1967	17(2)	33(4)	22(3)	14(2)	15(3)	52(8)
1968	6(1)	36(4)	24(3)	12(2)	26(4)	38(4)
1969	28(4)	19(3)	44(3)	51(5)	57(6)	69(5)
1970	29(4)	31(11)	34(4)	22(6)	22(4)	24(2)
1971	14(2)	11(4)	6(4)	40(6)	39(6)	46(10)
1972	20(3)	48(8)	62(9)	48(4)	62(6)	31(6)
1973	47(12)	28(7)	39(4)	30(6)	28(8)	32(9)
1974	26(3)	26(5)	40(4)	58(9)	70(5)	42(4)
1975	26(5)	21(3)	55(4)	54(6)	70(4)	44(4)
1976	10(2)	48(22)	32(6)	62(9)	64(6)	57(6)
1977	25(4)	43(5)	15(4)	13(5)	21(4)	39(6)
1978	21(3)	38(4)	34(6)	54(6)	23(3)	62(11)
1979	27(4)	35(6)	30(4)	38(6)	45(5)	40(6)
1980	28(6)	24(5)	37(4)	15(3)	57(5)	31(4)
1981	12(5)	19(3)	14(3)	29(5)	42(5)	51(4)
1982	18(2)	21(5)	39(5)	28(3)	46(5)	87(23)
1983	71(5)	97(5)	87(4)	110(10)	124(5)	125(14)
1984	4(10)	31(7)	49(15)	41(15)	-11(15)	32(8)

	Jul	*Aug*	*Sep*	*Oct*	*Nov*	*Dec*
1953	41(13)	53(4)	29(6)	33(8)	32(7)	8(8)
1954	6(6)	38(10)	17(6)	-8(4)	15(8)	25(12)
1955	46(10)	2(11)	8(5)	-9(8)	9(4)	2(5)
1956	69(11)	35(10)	49(7)	21(4)	69(8)	-9(3)
1957	111(19)	39(11)	54(7)	42(3)	35(4)	18(6)
1958	56(6)	35(3)	31(4)	40(5)	21(4)	27(5)
1959	26(2)	12(3)	30(7)	24(11)	13(1)	2(1)
1960	38(3)	28(3)	28(2)	23(4)	27(5)	20(5)
1961	34(5)	37(2)	28(2)	18(2)	27(2)	14(2)
1962	33(2)	27(2)	26(3)	24(2)	28(2)	15(2)
1963	40(3)	38(4)	43(3)	37(4)	36(4)	24(3)
1964	40(4)	37(4)	31(3)	30(3)	17(3)	27(3)
1965	60(4)	64(5)	36(3)	29(4)	36(2)	33(3)
1966	53(3)	29(2)	32(2)	26(2)	19(2)	13(1)
1967	36(2)	34(4)	22(2)	19(4)	24(3)	26(3)
1968	63(6)	29(3)	34(3)	29(2)	22(2)	33(6)
1969	41(4)	43(4)	31(4)	16(3)	10(1)	15(3)
1970	19(3)	23(3)	21(3)	15(3)	19(2)	15(3)
1971	39(4)	44(6)	31(7)	34(5)	19(3)	31(5)
1972	66(10)	105(10)	70(12)	40(4)	37(5)	42(8)
1973	42(7)	27(6)	29(4)	31(5)	15(5)	15(4)
1974	61(3)	32(3)	25(5)	28(5)	37(4)	33(7)
1975	54(6)	54(6)	23(5)	18(3)	4(2)	16(3)
1976	74(5)	30(17)	50(4)	45(7)	38(6)	34(3)
1977	48(6)	32(4)	19(3)	48(7)	23(2)	18(2)
1978	36(12)	30(9)	32(3)	31(5)	25(6)	24(4)
1979	39(4)	26(3)	37(3)	27(4)	37(7)	20(5)
1980	28(4)	29(4)	28(3)	34(6)	20(4)	15(4)
1981	41(6)	29(3)	27(4)	21(3)	21(3)	19(2)
1982	71(9)	30(6)	34(10)	59(4)	66(5)	68(10)
1983	91(8)	18(15)	46(17)	40(4)	42(7)	15(10)
1984	54(8)	37(5)	54(20)	19(8)	13(17)	26(8)

Table 11. Net atmosphere - ocean heat exchange, Q_N. The standard error of the mean appears in parentheses to the right of each mean value. Units are watts/m^2. (Values may be converted to units of cal cm^{-2} day^{-1} by multiplying by the factor 2.064.)

	Jan	Feb	Mar	Apr	May	Jun
1953	220(13)	193(13)	196(13)	152(24)	51(16)	142(10)
1954	261(11)	187(10)	200(9)	247(9)	101(8)	89(10)
1955	194(13)	273(11)	164(22)	211(16)	192(20)	115(8)
1956	208(12)	286(25)	232(22)	150(15)	137(18)	79(9)
1957	258(11)	143(16)	176(16)	125(17)	103(11)	63(16)
1958	203(7)	146(9)	189(15)	171(10)	110(16)	81(8)
1959	236(7)	215(9)	155(13)	139(13)	125(18)	92(9)
1960	228(8)	220(4)	209(6)	182(5)	153(4)	113(7)
1961	211(5)	221(4)	193(7)	175(4)	133(7)	83(6)
1962	210(5)	195(5)	216(6)	177(6)	135(6)	69(4)
1963	219(7)	213(5)	185(5)	156(0)	100(6)	88(3)
1964	196(6)	192(4)	199(6)	156(10)	111(11)	104(10)
1965	190(8)	187(8)	164(4)	135(7)	35(9)	69(6)
1966	188(7)	179(7)	187(6)	145(9)	108(6)	86(5)
1967	183(5)	202(6)	196(4)	187(4)	157(5)	62(9)
1968	214(5)	196(5)	207(4)	196(4)	118(6)	86(5)
1969	195(6)	209(6)	164(5)	134(7)	82(10)	41(8)
1970	185(8)	212(13)	203(7)	184(10)	130(7)	101(3)
1971	220(5)	219(8)	230(7)	155(9)	99(9)	67(13)
1972	205(5)	188(12)	150(11)	142(7)	77(10)	99(10)
1973	173(16)	203(11)	172(7)	171(11)	153(11)	95(13)
1974	197(6)	211(8)	187(6)	128(13)	63(7)	75(5)
1975	187(8)	217(6)	157(7)	138(9)	62(7)	66(6)
1976	215(6)	166(22)	179(9)	124(14)	78(9)	58(8)
1977	209(9)	174(6)	210(9)	218(9)	142(7)	92(9)
1978	209(8)	185(7)	200(9)	130(10)	139(7)	64(15)
1979	213(8)	204(9)	192(7)	166(10)	101(8)	82(9)
1980	198(9)	217(8)	184(6)	190(8)	99(8)	103(6)
1981	211(8)	202(6)	214(5)	166(9)	114(7)	75(5)
1982	207(5)	220(9)	182(6)	172(5)	111(7)	26(31)
1983	161(8)	139(7)	121(7)	66(14)	8(6)	-8(17)
1984	240(14)	213(11)	180(17)	158(19)	197(24)	101(14)

	Jul	Aug	Sep	Oct	Nov	Dec
1953	91(26)	74(6)	151(11)	171(16)	157(14)	227(19)
1954	135(14)	93(15)	138(9)	201(8)	183(19)	143(16)
1955	58(14)	152(18)	140(9)	222(15)	215(13)	226(17)
1956	34(15)	97(15)	109(8)	166(9)	98(13)	245(22)
1957	12(23)	110(18)	108(12)	144(6)	158(7)	200(9)
1958	69(12)	112(6)	127(8)	149(9)	198(8)	204(11)
1959	104(5)	139(6)	140(11)	174(18)	189(5)	224(5)
1960	95(5)	120(6)	129(4)	152(7)	172(12)	193(7)
1961	80(7)	103(4)	130(3)	173(5)	189(4)	203(5)
1962	89(3)	111(3)	140(6)	157(4)	167(4)	211(5)
1963	83(5)	106(7)	120(6)	155(7)	155(7)	183(8)
1964	78(6)	102(7)	138(5)	145(4)	173(6)	198(5)
1965	58(7)	66(7)	121(5)	154(6)	161(4)	180(5)
1966	70(5)	114(4)	131(3)	151(3)	166(4)	200(4)
1967	85(4)	97(5)	144(5)	169(7)	156(5)	196(6)
1968	55(9)	108(4)	135(5)	157(5)	174(4)	192(7)
1969	75(6)	93(6)	121(6)	170(5)	192(4)	203(5)
1970	102(4)	117(5)	146(5)	165(5)	195(5)	198(7)
1971	71(6)	92(10)	128(11)	142(8)	194(6)	176(9)
1972	51(15)	23(13)	98(17)	145(7)	147(8)	171(10)
1973	77(11)	120(10)	144(7)	157(9)	187(9)	191(7)
1974	46(5)	106(6)	141(7)	175(9)	166(8)	183(12)
1975	63(8)	79(10)	144(8)	178(5)	197(5)	195(6)
1976	52(8)	116(25)	122(8)	148(9)	162(9)	195(7)
1977	72(9)	111(6)	156(7)	131(10)	181(4)	222(7)
1978	89(16)	118(14)	138(6)	158(8)	191(10)	208(7)
1979	86(7)	133(6)	131(6)	171(7)	158(10)	207(10)
1980	105(8)	117(7)	154(6)	156(10)	192(9)	220(9)
1981	83(8)	119(6)	139(5)	191(6)	196(5)	207(4)
1982	59(12)	114(8)	144(14)	132(6)	129(7)	155(13)
1983	34(10)	139(19)	136(25)	145(7)	184(15)	216(15)
1984	78(12)	108(10)	121(36)	166(14)	228(25)	190(11)

uncommon in the figure with the notable exception of the early 1970s and again in the early 1980s. The main point is that features in Fig. 4L seem unrelated to any major features apparent in the other series plotted in Fig. 4. Thus, the major effect of uneven distribution of reports appears to be in increasing sampling variance rather than in introducing long-term nonhomogeneity in the various time series.

Discussion

Since the 12-month running mean filter used to highlight the long-term variations in Fig. 4 incorporates no data more than 6 months previous or following, the indicated multiyear features are certainly real, and in no way represent artifacts of filtering and smoothing procedures. Moreover, the interyear variations of annual mean values tend to be of similar magnitude to the cyclic seasonal components (Figs. 2 and 3), making the separation of these scales in analysis of effects (e.g., on the biota) a difficult problem. For example, the impact of long-term variability will generally depend on phase relationships with the seasonal variation. Additional complications involve the adaptations of the biota, not only the long-term evolutionary adaptations of life cycle processes to regular cyclic effects, but also lagged responses of community composition, etc., to events of the recent past (see Mendelsohn and Mendo, this vol.).

This area of the world's ocean may be uniquely troublesome in these respects. Because the Pacific Ocean is so large, it is much less subject to continental effects which amplify seasonalities due to the low heat storage capacities of continents relative to oceans. The apparent consequence is much less forcing of Pacific Ocean processes to follow a regular seasonal cycle than may be the case, for example, in the Atlantic; the result is the dominance of interyear variation in the Pacific (Picaut 1985). The location so near to the eastern terminus of the equatorial wave guide results in a focusing of variability initiated in various portions of the great Pacific ocean-atmosphere coupled system to particularly impact the ocean habitat off Peru. Indeed, this may constitute part of the explanation for the enormous biomasses of pelagic fishes that have inhabited the region; i.e., because of the intense irregular environmental variability, a single, rather unspecialized fish species with very rapid population responses may be able to dominate the system relatively free from predation and competition from more specialized, less responsive species that would be more subject to the inefficiencies of multiple food-chain steps.

We have noted that the interyear variations tend to involve groups of years. In fact single features, e.g., the 1982-1983 El Niño, the 1954-1955 cold period, etc., so dominate the series that the entire series length becomes a dominant scale of variability. The result is that any sort of assumption of stationarity must be somewhat unrealistic; the real degrees of freedom useful for empirical analysis nearly vanish with respect to such features. It is also apparent from even casual inspection of Fig. 4 that the index series presented in this paper are all highly interrelated in terms of major interyear features, further exacerbating the problems of empirically sorting the various effects. Any available mechanistic constraints, provided by established physical or biological principles, that can be imposed on empirical analysis, would of course be very helpful in this situation.

Variable vs. Constant Transfer Coefficient Formulations

Some differences in the results of variable and constant transfer coefficient formulations in the wind stress estimates (Equation 1) and in the estimates of certain of the heat exchange components (Equations 4, 5 and 6) have been noted in the discussions of both seasonal and interyear variability. The differences have mainly been in magnitude of the particular index, with temporal aspects of the variability appearing to be relatively unaffected. An exception was the conductive component of heat exchange, Q_C, where the effect of stability in the atmospheric boundary layer introduced major discrepancies between the alternate formulations (Fig. 3E). Fortunately, Q_C is by far the smallest heat exchange component. Some summary information concerning gross effects of the differences in the various series with respect to time series properties is indicated in Fig. 5.

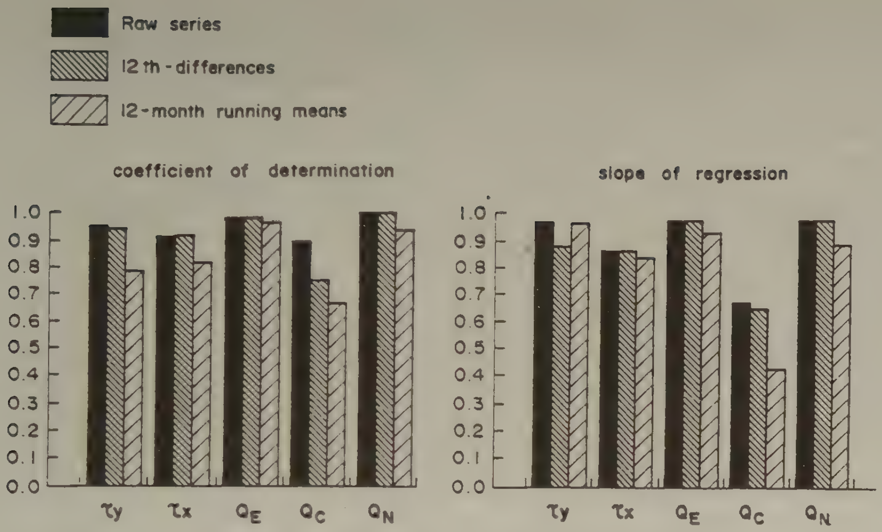

Fig. 5. Graphs of r^2 (= coefficient of determination, i.e., proportion of variation in one series 'explained' by other series) and slope of the regression of the variable transfer coefficient formulation versus the constant transfer coefficient formulation of alongshore stress (τ_x), onshore stress (τ_y), evaporative heat loss (Q_E), conductive heat loss (Q_C) and net atmosphere-ocean heat exchange (Q_N).

In the case of alongshore component of wind stress, the raw monthly series computed according to the two types of drag coefficient formulation are well correlated, each accounting for more than 95% of the variance in the other. When 12th-differencing was employed to remove the cyclic seasonal variations, the correlation dropped only slightly; this lower than expected drop in r^2 must be due to a strong seasonality in the differences resulting from the two formulations. Note that both the raw and 12th-differenced series pairs were much more highly correlated than the pair of 12-month running mean filtered series (which can be viewed in terms of directly proportional offshore Ekman transport in Fig. 4G). The slope of the regression of the variable coefficient alongshore stress series on the constant coefficient series is nearly one to one in the raw series; it drops to below 0.9 in the 12-differenced series, but is above 0.95 in the filtered series.

Slightly lower degrees of relationship are seen for the onshore component which tends to be much the smaller of the two stress components. The respective formulations of evaporative heat loss (Q_E) were very highly correlated in raw and 12th-differenced series. The degree of relationship fell only slightly after the 12-month running mean was applied. In the case of the conductive heat loss term (Q_C), the two formulations gave substantially greater differences, particularly after 12th-differencing or filtering. In the case of net heat exchange (Q_N) the differences between the results of the two formulations appear not to be appreciable. Note that in all cases the raw and 12-differenced series were more highly correlated between the constant and variable coefficient formulations than were the corresponding 12-month running mean filtered versions of the respective series; thus the degree of relationship is even higher in the case of the unsmoothed series, even after the seasonality is removed, than can be seen in the comparative examples of filtered series in Fig. 4.

In view of the time series similarities, the constant transfer coefficient versions of the respective index series are the only ones presented herein in tabular form (Tables 5, 6, 10 and 11). In view of the larger relative effect of the uncertainties as to proper formulation of the transfer coefficient for conductive heat loss, and because its very small magnitude makes it relatively unimportant in any case, no tabular series of Q_C is included. Of course, it would be possible to assemble the constant coefficient version of the Q_C series from the values in Tables 8 to 11.

Offshore Ekman Velocity of the Mixed Layer

In discussing the inference of Parrish et al. (1983) that the offshore Ekman transport should ideally be divided by the effective mixed layer depth, to yield the net rate of offshore transport of drifting larvae which are passively mixed through the layer, Bakun (1985) stressed the importance of the qualification "ideally". Ekman transport is estimated from relatively abundant surface wind reports, which reflect the fairly large spatial scales of atmospheric variation. Mixed layer depth may vary on much shorter oceanic length scales and must be determined from generally much less abundant subsurface observations. In cases where the estimate of effective mixed layer depth may be very imprecise, the derived estimate of offshore Ekman velocity of the mixed layer could constitute a less reliable indicator of variability in this process than the Ekman transport alone.

On long time scales, mixed layer depth and wind stress observations are likely to be substantially correlated. However, within any given month it is probably not too bad an assumption to regard observations used to estimate these quantities (surface wind and subsurface temperature structure) as largely independent samples of the respective monthly distributions, particularly since there will normally be many more surface than subsurface reports. In this case, combining the standard errors according to the rules for a quotient of independently observed quantities (e.g., Beers 1953) should provide a reasonable gauge of precision. Thus the ratio of the standard error to the monthly mean derived net offshore Ekman velocity of the mixed layer might be reasonably estimated as being equivalent to the square root of the sum of the squares of the respective ratios of the standard errors to the monthly mean values of the Ekman transport and mixed layer depth components of the calculation.

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8706

Annotated List of Shark Attacks in the Hawaiian Islands—July 1987

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Case No.	Date	Location	Victim	Circumstances
1*	1779	Maliu, Hawai'i	Nu'u-anu-pa'ahu	Young male gashed on one side of buttocks after being pursued while surfboarding. Subsequently suffered "great pain" and died at Pololu.
2*	1828	Lahaina, Maui	Male	"A man out riding surf at 'Uo was killed by a shark which bit off his limbs and left his body floating." Attack witnessed by a number of Hawaiian chiefs.
3*	June 2, 1886	Hamakua, Hawai'i	Two females	Washed into the sea while fishing from shore; one woman found bitten (fatal), the other woman disappeared.
4	Early 1900's	Inter-Island Dry Dock at Kaka'aka Street, Honolulu, O'ahu	Emil A. Berndt	Young boy severely chaffed when a large shark swam between his legs.
5*	Aug. 8, 1902	Kalihi, O'ahu	Young male	Pulled under while crabbing; both arms amputated.
6*	1904	Honolulu, O'ahu	Male	Unprovoked attack, but unable to determine circumstances.
7*	1907	Pepe'ekeo, Honomu, Hawai'i	Male	Bitten while fishing.
8	Oct. 8, 1907	Kalepolepo, Kihei, Maui	Male	Arm amputated at the elbow while retrieving fish caught in net.
9*	Jan. 17, 1908	Mana, Kaua'i	Male	Pulled under while gathering fish stunned by dynamite.
10*	Apr. 10, 1909	Pa'uwela, Maui	Mrs. Ah Kim Chong	Nineteen-year-old woman reported to have been swept away by waves while gathering 'opihi along the rocky shoreline. Search party saw a large shark devour what appeared to be part of the missing woman's body.
11	April 1910	Pearl Harbor, O'ahu	Martin Lund	Unprovoked attack, but unable to determine circumstances.
12*	1910	Hilo, Hawai'i	Male	Bitten while fishing.
13*	March 3, 1914	Honomu, Hawai'i	Okomoto	Washed into the sea while picking 'opihi; attacked by two large sharks.
14	Sept. 28, 1922	Keawanui, Kamalo, Moloka'i	Male	Bitten while inspecting wharf.
15	April 7, 1926	Hilo Bay, Hawai'i	Mrs. Leonard Carlsmith	Bitten while swimming in turbid water near yacht club; severe lacerations on leg; 6-ft shark observed in area.
16*	May 18, 1926	Hale'iwa, O'ahu	William J. Goins	Gave a sudden shriek, then disappeared while swimming at Hale'iwa; remains of body found in 12.5-ft great white shark caught of Kahuku.
17*	Sept. 2, 1931	Kahala, O'ahu	George Gaspar	Swept out to sea by strong currents while fishing; remains of body found in 18-ft shark caught off Barber's Point.

18	Feb. 16, 1932	Lahaina, Maui	Male	Sailor from U.S. Navy vessel *SARATOGA* bitten while swimming about 1 mile off Mala Wharf. Two wounds, each 6 inches long, were inflicted.
19	Oct. 4, 1939	Kane‘ohe Bay, Mokapu, O‘ahu	James Akina	Bitten on hand by 5-ft shark while spearfishing in shallow water.
20	July 1, 1941	Nanakuli, O‘ahu	Hisao Shimoto	Bitten on arm while removing 100-lb shark from fishing line.
21*	June 1943 (?)	Ma‘alaea, Maui	Male	Soldier's shorts and an arm recovered from a shark caught at Ma‘alaea. Items seen at the 22nd Army hospital in Makawao.
22	1943	Midway, Northwestern Hawaiian Islands	Male	Unprovoked attack, but unable to determine circumstances.
23	1943	Midway, Northwestern Hawaiian Islands	Male	Unprovoked attack, but unable to determine circumstances.
24	June 27, 1947	Makaha, O‘ahu	Valentine Limatoc	Bitten while spearfishing with six other men.
25	Sept. 19, 1948	Makapu‘u, O‘ahu	Noah Kalama	Bitten on leg while swimming.
26*	June 25, 1951	Kapehu Beach, Laupahoehoe, Hawai‘i	Alejandro Nodura	Swept out to sea while fishing from shore. Victim seen in shark's mouth.
27*	Aug. 3, 1952	Ala Moana, O‘ahu	Shigeichi Kawamura	Missing while swimming. Shark bite found on right side of body.
28*	Dec. 3, 1952	Ma‘ili, O‘ahu	Gerbacio Solano	Bitten on arm while swimming from fishing boat; shark reported to be in excess of 22 ft.
29	Feb. 18, 1953	Barber's Point, O‘ahu	James S. Takeuchi	Bitten on hand while removing shark from net.
30	July 4, 1953	Ka‘ula Rock	David Crick	Fell off boat while fishing; bitten on leg.
31*	Apr. 15, 1953	O‘ahu	Leonard Gaut	Unprovoked attack, but unable to determine circumstances.
32*	July 26, 1953	Ma‘ili, O‘ahu	Harold Souza	Bitten on thigh while spearfishing close to shore; 10-ft shark observed.
33	Sept. 2, 1953	Waiau, Pearl Harbor, O‘ahu	Daniel Gonsalves	Bitten on leg and foot by 5-ft hammerhead shark while crabbing.
34*	Apr. 8, 1954	Wailupe, O‘ahu	Gordon S. Chun	Missing while fishing from shore; body recovered in mutilated condition.
35	1954	Moloka‘i	Sevenno	Unprovoked attack, but unable to determine circumstances.
36	April 1955	Hilo, Hawai‘i	Kanematsu Oshiro	Bitten on hand while fishing from boat.
37	Sept. 20, 1955	East Moloka‘i	Phillip C. Diez	Bitten on arm while swimming.
38*	Dec. 13, 1958	Lanikai, O‘ahu	William S. Weaver	Leg amputated while surfing on an air mattress near Twin Islands; 15- to 25-ft shark (believed to be tiger shark) observed near body.
39	1950's	Waikiki, O‘ahu	David Lloyd	Provoked attack, but unable to determine circumstances.
40	Feb. 27, 1960	Makena, Maui	John Benjamin	Severe lacerations obtained while spearfishing.
41*	Dec. 27, 1960	Ma‘ili Point, O‘ahu	Harold Riley	Swept out to sea while net fishing; 20-ft shark observed attacking victim; body recovered off Nanakuli.
42	Aug. 2, 1961	Pearl Harbor, O‘ahu	Kazuhiko Kato	Bitten on hand by 8-ft shark while net fishing.
43*	Apr. 8, 1963	Hapuna Beach, Hawai‘i	Roy C. Kametani	Washed into the sea while picking ‘opihi; parts of body recovered.
44	Apr. 12, 1963	Awili, South Kona, Hawai‘i	Aiona Aka	Bitten on leg and foot while surfing; 12- to 15-ft shark observed.
45*	Sept. 20, 1967	Kailua, Bay, O‘ahu	Male	Victim lost at sea when boat capsized between O‘ahu and Moloka‘i; remains of body found in 11-ft tiger shark.
46	March 9, 1969	Makaha, O‘ahu	Licius Lee	Bitten on leg while surfing; identified as great white shark; dead whale recently removed from the area.
47	Nov. 11, 1969	Barber's Point, O‘ahu	D. R. McGinnis	Bitten on tank while scuba diving; abrasions on arms and legs resulting from contact with shark.
48*	1960's (?)	Off Lahaina, Maui	Danson Nakaima	Passed out while scuba diving for black coral at 180 ft. About 30 large sharks seen near remains of the body.
49*	Mar. 31, 1970	Waimea Bay, O‘ahu	Ernie Reathaford	Swept out to sea while body surfing; 15- to 18-ft shark observed.

13a

50	Oct. 24, 1970	Brennecke Beach, Poipu, Kaua'i	James C. Mattan	Bitten on shoulder and arm while body surfing.
51	Mar. 16, 1972	Waihe'e, Wailuku, Maui	Adam Gomes, Jr.	Bitten on leg while spearfishing.
52	Aug. 17, 1972	Waimanu, Honoka'a, Hawai'i	Eric Fotherby	Bitten on arm by 8-ft shark while spearfishing.
53	Jan. 9, 1973	Ho'okipa Beach, Pa'ia, Maui	Robert Sterling	Bitten on leg while surfing close to shore; 4- to 6-ft shark observed in area.
54	Dec. 18, 1973	Kalama Beach, Kihei, Maui	Gary W. Floyd	Bitten on leg while swimming close to shore.
55*	June 10, 1976	Kama'ole Beach Park No. 1, Kihei, Maui	Donald Gard	Bitten on foot and leg by 3- to 5-ft shark while swimming.
56*	July 20, 1976	Maha'ulepu, Koloa, Kaua'i	Stephen C. Powell	Missing while scuba diving; lower remains of body recovered.
57	Apr. 21, 1977	Ka'anapali, Maui	Ruskin Vest	Bitten on arm by 4-ft shark while swimming close to shore.
58	Nov. 27, 1978	'Ewa, O'ahu	Wendell Cabunoc	Bitten on arm while surfing; 8-ft shark observed.
59*	1979 (?)	South Kohala, Hawai'i	Elderly male	Disappeared while fishing from shore. Fire department divers only found a hand and a flashlight.
60	Aug. 4, 1980	Puamana, Lahaina, Maui	Mark Skidgel	Bitten on left side of body while surfing close to shore; identified as 14-ft tiger shark.
61*	May 24, 1981	Ha'ena Beach Park, Kaua'i	Roger B. Garletts	Missing while scuba diving at 60- to 80-ft; only diving equipment recovered, including shredded wet suit bearing numerous tooth marks. Victim reportedly spearfishing in murky, choppy water.
62*	June 12, 1982	Honoli'i Pali, Hilo Bay ('Alae Point), Hawai'i	Preston D. Soley	Retrieval of floating body hindered by 4-ft shark. Autopsy showed that death was probably from drowning. One-third of body missing due to bites by at least four sharks.
63*	Aug. 24, 1981	Keaukaha, Hilo, Hawai'i	Ernest Watson	Disappeared while fishing from shore. Leg found seven days later wedged in rocks 150 yd offshore.
64	Nov. 9, 1981	La'au Point, Molokai'i	Leo A. Ohai	Bitten on hand while untangling crab-trap line from propeller. Seven-foot shark had followed the boat for three days and reportedly was very unusual looking with a "flat head."
65	Dec. 13, 1981	Nimitz Beach, Barber's Point, O'ahu	Melvin T. Toma	Severely bitten on right leg by 12-ft tiger shark while swimming at the surface shortly after entering water; site located 300-400 yd offshore over depth of 20 ft. Looking for fish, but none had been taken when attack occurred.
66	Feb. 14, 1982	White Plains Beach, Barber's Point, O'ahu	Lisa Miller	Bitten on left leg while wading in 3- to 4-ft of water; 17 stitches required.
67	Feb. 14, 1982	White Plains Beach, Barber's Point, O'ahu	Female	Bitten on right foot while swimming in shallow water.
68	June 13, 1982	Ho'okipa Beach, Pa'ia, Maui	Scott Shoemaker	Severely bitten three times on the thigh after falling into water while sailboarding 100 yd outside the breakers. Required 120 stitches.
69	June 3, 1984	Kane'ohe Bay, O'ahu	Susan Buecher	Bitten on the foot while being pulled on a plastic ski board by a swimmer. Incident happened at 1700 '. in water 5-ft deep, about 400 yd from shore. Numerous stitches and a cast required.
70	Oct. 12, 1985	Barber's Point, O'ahu	Dominic Dela Cruz	Severe gashes to left arm requiring surgery. Attack occurred off Barber's Point Lighthouse while floating on an inner tube after diving for lobster
71	Oct. 18, 1985	Princeville, Kaua'i	Joe Thompson	Right hand and forearm amputated by a large shark while boogie-boarding. Believed to be a tiger shark.
72*	Apr. 20, 1986	Kalihiwai, Kaua'i	Levi Chandler	Fell from rocks and disappeared while fishing at Kalihiwai Point. Pieces of clothing and human flesh were recovered by fire department divers who encountered a large shark
73*	Apr. 15, 1987	Kailua-Kona,	Daniel Kennedy	Last seen swimming from shore out to an anchored sailboat. Swimming trunks found bitten in half on the bottom

* FATAL

8707

Maturity of Widow Rockfish *Sebastes entomelas* from the Northeastern Pacific, 1977-82

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ABSTRACT

Gonad development, size, age, calculated weight at maturity, and fecundity for the widow rockfish (*Sebastes entomelas*) are reported. In 1977-82, a total of 3,636 specimens were examined from commercial trawl and partyboat sport catches off Oregon and California. Gonad development was earlier in southern latitudes. The principal months of parturition were February-March off Oregon and January-February off California. Mean size, age, and calculated mean weight at 50% maturity were 33 cm fork length (FL), 4 years of age, and 534 g for Oregon males, compared with 32 cm FL and 5 years for California males. Oregon females were 50% mature at 38 cm FL, 7 years of age, and 937 g, as compared with 33 cm FL and 5 years for California females. Over 99% of the males and 92% of the females randomly sampled from Oregon landings were mature, compared with 93% males and 94% females from California landings. Fecundity increased with increasing length and ranged from 95.000 to 1.113.000 eggs in Oregon samples.

INTRODUCTION

Research on the life history of the rockfishes has focused primarily on commercially important species (Sorokin 1958, 1967; Shiokawa 1962; Moser 1967; Gunderson 1977) or species in a nearshore habitat (Berge and Schultz 1973; Miller and Geibel 1973; Hallacher 1976; Hobson and Chess 1976; Larson 1977). Some life history information on the widow rockfish (*Sebastes entomelas*) occurs incidentally in studies using market samples (DeLacy and Dryfoos 1962; DeLacy et al. 1964; Phillips 1964) and in trawl surveys (Harling et al. 1971; Hitz 1962; Westrheim 1975; Westrheim and Harling 1975). The species has only recently been focused upon, due to a new and rapidly expanding fishery. In 1979 a target fishery began on widow rockfish off Oregon and California by large domestic trawlers using pelagic trawls. Life history information on these populations is being investigated while the fishery is still young.

The reproductive biology of widow rockfish was investigated to determine months of spawning (parturition) and age and size of sexual maturity for each sex. This information provides a baseline for examination of possible changes in the populations, such as sexual maturity at younger ages as fishing reduces the density of fish. Field studies were conducted to determine age, length, and weight at sexual maturity by sex for widow rockfish landed by the commercial fleet in Oregon during 1979-80. Life history information on *Sebastes* spp. was collected from the sport and commercial fleets in California beginning in 1977, and the program was expanded in 1980 to include reproductive biology. This information has been used to examine reproductive biology of widow rockfish and to make comparisons between the Oregon and California populations.

METHODS

Life history and maturity data were acquired by sampling rockfish in the Oregon commercial fishery and in the California commercial and sport fisheries. The Oregon phase of the sampling began in 1979 on commercial trawl catches made from Cape Blanco to the Columbia River. Since 1979, data collected included fork length, sex, otolith and gonad stage, and descriptions of gonads of individual fish. Individual weight to the nearest 10 g was added to the data collected in December 1979. Information on stomach contents was taken frequently in 1980. Sixty-eight ovaries were collected in December 1980 and January 1981 and processed as described by Boehlert et al. (1982). Samples of approximately 30 fish were taken from commercial landings at least once a month when available. In 1979, 14 random samples were taken, comprised of 195 females and 209 males. In 1980, 31 random samples were taken, comprised of 446 females and 475 males. An additional 49 females and 81 males were selectively sampled because they were either very small or large specimens, and they were were needed to supplement the random samples. Sampling began in 1977 on sport catches made in California. Data were collected on morphometrics, meristics, sex, gonad stage, and age (otoliths) for all rockfish species and included 42 male and 80 female widow rockfish. California maturity data collection was expanded in March 1980 on catches made from Eureka to Morro Bay. Random samples of the sport and commercial fisheries contained 15-20 fish per sample for all *Sebastes* spp. landed. Data collected included total length, sex, otoliths, gonad stage, interstitial fat, and stomach contents from 832 male and 1,227 female widow rockfish. Total length (TL) was converted to fork length (FL) by the equation $FL = 6.1635 + 0.9341(TL)$ for comparing Oregon and California data (Lenarz 1987).

The Oregon maturity criteria used to describe gonad condition were modified from Westrheim (1975) and Gunderson (1977) and are shown in Table 1. California maturity stages were determined in the laboratory after the gonads were preserved in 10% formalin. The criteria (Table 2) were similar to those used in Oregon.

RESULTS

Timing of gonad development

The reproductive biology of the genus *Sebastes* is similar in all species that have been investigated (Eigenmann 1892; Sorokin 1967; Moser 1967; Westrheim 1975). *Sebastes entomelas* is ovoviviparous; that is, ova are retained within the ovaries after internal fertilization and contain enough yolk so that no additional nutritive material is supplied to the embryos by the female parent (Hickman 1961; DeLacy et al. 1964; MacGregor 1970). Gestation usually lasts from 1-3 months. Gaseous embryonic wastes are eliminated through the highly vascularized gonad (Moser 1967). While Moser (1967) and MacGregor (1970) reported that some members of the genus have two broods per season, most *Sebastes* species spawn once annually (Westrheim 1975). Widow rockfish have a well defined period of egg development and spawn once a year, as shown by our data and by the absence of secondary oocytes as reported by Boehlert et al. (1982).

Samples of Oregon catches indicated that copulation occurred primarily in December. Eggs were fertilized about a month following copulation. Embryos developed at nearly the same rate, and parturition occurred about 1 month following fertilization. Widow rockfish are live bearers, and we observed fish containing large numbers of tiny free larvae.

Gonad development of widow rockfish occurred earlier in southern latitudes as indicated by the principal months of parturition (Table 3). Mature Oregon widow rockfish testes were noticeably swollen in June and contained some noticeable milt in August (Fig. 1). Mature females off Oregon began to display enlarged grey ovaries with opaque white eggs in September. In October as the ovaries enlarged, they become pinky-white in color. By January many females contained colorless, translucent fertilized eggs. Eyed eggs and larvae appeared in February and spawning (parturition) was completed in March.

Gonad development in California fishes begins about a month earlier than in Oregon, with mating during September, fertilized eggs occurring in November, and spawning completed during February (Fig. 1). The trend of later parturition in northern latitudes is confirmed with data from British Columbia where spawning occurs during April (Westrheim 1975). There is a time lag of 1 to 2 months between copulation and fertilization. Hence there is the possibility of sperm storage by the female.

Sexual maturity by age, length, and weight

Fifty percent sexual maturity for female widow rockfish occurred at an earlier age and smaller length in southern fishing areas (Table 4). Males appeared to mature sexually at a smaller length and younger age than females off Oregon.

First sexual maturity for males occurred at age 3 yr in Oregon samples (Table 5) and age 3 in California samples (Table 6). Mature females were first seen at age 5 in Oregon samples and age 3 in

Table 1—Gonad condition criteria applied to *Sebastes entomelas* from Oregon landings, 1979-80.

	Code	Condition	Description
Males	1	Immature	String-like, colorless, translucent, very small
	2	Maturing	Slight swelling, translucent, white, small
	3	Mature	Ribbon-like, swolen, brown to white
	4	Developing	Large, swollen, easily broken, milt in sperm duct
	5	Spawning	Swollen, flowing milt when pressure applied to testes
	6	Spent	Swollen, milt in sperm duct
	7	Resting	Ribbon-like, flat, tan or brown
Females	1	Immature	String-like, very small, firm, translucent
	2	Maturing	Small, greyish white, translucent or opaque
	3	Mature	Large, opaque, granular, grey to pink-white, ova held in follicle
	4	Developing	Fertilized, large, translucent (cleared) eggs with pink cast or colorless, ova usually not held in follicle
	5	Spawning	Eyed eggs and/or larvae, ova not held in follicle, large, contains much fluid
	6	Spent	Flaccid, purple to pink ovary, flattened elliptical in cross section
	7	Resting	Moderate size, firm, red-grey ovary

Table 2—Gonad condition codes applied to *Sebastes entomelas* from California landings.

Code	Males	Code	Females
1	Immature	1	Immature
2	Maturing	2	Maturing
3	Mature	3	Mature
		4	Fertilized (developing)
		5	Eyed larvae (spawning)
		6	Spent
7	Resting	7	Resting

Table 3—Principal months of parturition by area for *Sebastes entomelas*.

Area	Month
California	January-February
Oregon	February-March
British Columbia[1]	April

[1] from Westrheim (1975)

Table 4—Percent maturity for Oregon, California, and British Columbia *Sebastes entomelas* by age, size, and weight.

		Males			Females		
	Maturity %	Age (yr)	Length (cm)	Weight (g)	Age (yr)	Length (cm)	Weight (g)
Oregon	>0	3	31	444	5	35	662
	50	4	33	534	7	38	937
	100	8	38	870	9	43	1150
California	>0	4	25	—	4	25	—
	50	5	32	—	5	33	—
	100	8	46	—	8	46	—
British Columbia[1]	50	—	37	—	—	38	—

[1] from Westrheim (1975)

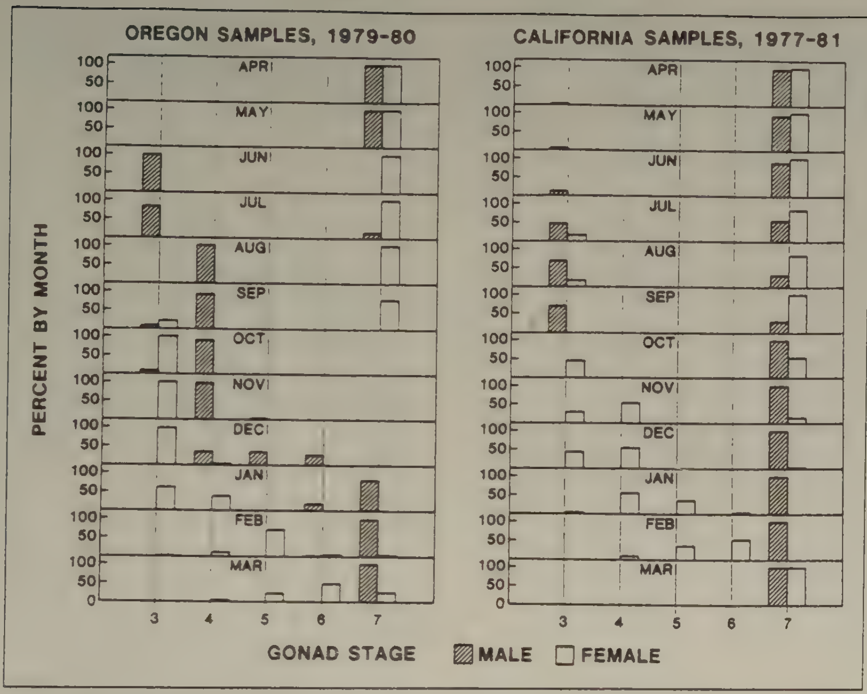

Figure 1—Gonad condition of *Sebastes entomelas* by month from Oregon samples, 1979-80, and from California samples, 1977-81. See Appendix for actual percent distribution of Oregon random samples.

Table 5—Maturity by age and sex for *Sebastes entomelas* for Oregon samples, 1979-80 (includes random and nonrandom age samples).

	Number				%	
	Immature		Mature		Mature	
Age (yr)	M	F	M	F	M	F
3	0	—	1	—	100	—
4	6	4	5	0	46	0
5	10	23	29	4	74	15
6	1	10	21	2	96	17
7	2	3	16	7	89	70
8	0	6	59	23	100	79
9	2	8	196	150	99	95
10	0	6	187	217	100	97
11	0	2	74	73	100	97
12	0	0	41	36	100	100
13	0	0	15	19	100	100
14	0	0	7	15	100	100
15	0	0	8	10	100	100
16	0	0	4	8	100	100
17	0	0	3	3	100	100
18	0	0	1	4	100	100
19	—	0	—	4	—	100
20	—	0	—	4	—	100
21	—	0	—	1	—	100
22	—	0	—	2	—	100
23	—	0	—	2	—	100
Total no.	21	62	667	584		

Table 6—Maturity by age and sex for *Sebastes entomelas* from samples off California, 1977-82.

	Number				%	
	Immature		Mature		Mature	
Age (yr)	M	F	M	F	M	F
2	1	1	—	—	—	—
3	9	13	3	2	25	13
4	17	23	4	6	19	21
5	9	14	24	25	73	64
6	9	5	36	44	80	90
7	5	5	40	45	90	90
8	1	—	38	41	97	100
9	—	1	55	62	100	98
10	4	—	96	124	96	100
11	2	2	139	160	99	99
12	2	3	120	152	98	98
13	—	4	65	122	100	97
14	—	—	54	97	100	100
15	—	1	28	78	100	99
16	—	—	37	73	100	100
17	—	—	17	46	100	100
18	—	—	10	41	100	100
19	—	—	8	19	100	100
20	—	—	6	10	100	100
21	—	—	2	8	100	100
22	—	—	1	10	100	100
Total no.	59	72	783	1165		

California samples. Males from Oregon samples were 50% mature at about age 4 and 100% mature at age 8. California males were 50% and 100% mature at about age 5 and 8, respectively. Oregon female widow rockfish were 50% and 100% sexually mature at about age 7 and 9, respectively. Off California, females reached 50% and 100% sexual maturity at about age 5 and 8, respectively.

Off Oregon, males began to mature sexually at about 31 cm FL, with 50% mature at 33 cm, most mature at 36 cm, and all mature at 38 cm (Table 7). Females began to mature at 35 cm, and were 50% mature at about 38 cm and almost 100% mature at 42 cm.

Widow rockfish sexual maturity off California began at about 25 cm for males and 26 cm for females (Table 8). Most males and females were mature at 38 cm, but all fish may not have been mature until they were about 46 cm.

Westrheim (1975) reported that length at 50% maturity in the area of West Vancouver Island was 37 cm for males and 38 cm for females.

Calculated mean weight at first sexual maturity was 444 g for males and 662 g for females from Oregon samples (Table 4). Respective weights at 50% and 100% maturity were calculated at 534 g and 870 g for males and 937 g and 1,150 g for females.

Maturity of fish taken by Oregon trawl fishery

Most widow rockfish were sexually mature in the random samples from Oregon commercial trawl landings in 1979-80. By number, about 99% of the males and over 92% of the females were mature (Table 9).

Fecundity

Boehlert et al. (1982) reported on the fecundity of widow rockfish from Oregon samples taken in December 1980 and January 1981. Fecundity increased with increasing length, weight, and usually age. Estimates of fecundity ranged from 95,375 oocytes at 33 cm FL to 1,113,000 oocytes at 52 cm FL. The fecundity-length and fecundity-weight relationships were as follows.

Length $F = 59{,}182.4\ L - 1{,}999{,}200;\ r^2 = 0.90;\ N = 64$

Weight $F = 605.71\ W - 261{,}830.7;\ r^2 = 0.91;\ N = 64$

where F = fecundity, L = fork length (cm); W = weight (gm), r^2 = coefficient of determination, and N = number of specimens.

Table 7—Maturity by fork length and sex for *Sebastes entomelas* from Oregon trawl catches, 1979-80. Selected fish included.

Length (cm)	Number				% Mature	
	Immature		Mature			
	M	F	M	F	M	F
29	—	1	—	0	—	0
30	—	—	—	—	—	—
31	0	—	2	—	100	—
32	3	1	1	0	25	0
33	6	6	6	0	50	0
34	3	10	6	0	67	0
35	5	14	26	1	84	7
36	2	11	51	1	96	9
37	2	14	56	8	97	36
38	0	6	87	15	100	71
39	0	3	123	26	100	90
40	1	4	119	52	99	93
41	0	5	100	83	100	94
42	0	1	65	83	100	99
43	0	0	39	101	100	100
44	0	0	18	70	100	100
45	0	0	10	61	100	100
46	0	0	6	32	100	100
47	0	0	1	21	100	100
48	0	0	1	16	100	100
49	—	0	—	17	—	100
50	—	0	—	12	—	100
51	0	0	1	7	100	100
52	—	0	—	3	—	100
53	—	0	—	1	—	100
54	—	0	—	1	—	100
Total no.	22	76	718	611		

Table 8—Maturity by fork length and sex for *Sebastes entomelas* from California, 1977-82.

Length (cm)	Number				% Mature	
	Immature		Mature			
	M	F	M	F	M	F
23	2	1	—	—	0	0
24	1	—	—	—	0	0
25	1	1	1	—	50	0
26	1	1	4	1	80	50
27	2	4	1	3	33	43
28	6	7	1	1	14	13
29	3	7	1	—	25	0
30	5	8	4	3	44	27
31	6	8	2	4	25	33
32	4	3	5	2	56	40
33	1	4	3	6	75	60
34	2	2	6	6	75	75
35	5	1	6	7	55	88
36	3	6	13	9	81	60
37	6	4	10	16	63	80
38	2	2	23	10	92	83
39	4	1	35	19	90	90
40	2	—	59	21	97	100
41	2	1	81	28	98	97
42	1	1	121	35	99	97
43	5	2	158	47	97	96
44	1	2	122	75	99	97
45	2	1	87	133	98	99
46	—	—	40	145	100	100
47	—	—	19	137	100	100
48	—	—	3	140	100	100
49	—	—	2	164	100	100
50	—	—	—	116	—	100
51	—	—	—	67	—	100
52	—	—	—	28	—	100
53	—	—	—	10	—	100
54	—	—	—	2	—	100
Total no.	67	67	807	1235		

Table 9—Sexual maturity by number in random samples of *Sebastes entomelas* from Oregon trawl landings, 1979-80.

	1979		1980	
	Male	Female	Male	Female
No immature	1	14	4	25
No mature	208	181	475	421
% mature	99.5	92.8	99.2	94.4

The length-fecundity and weight-fecundity relationships described by Boehlert et al. (1982) differed significantly from data presented by Phillips (1964) on California widow rockfish. Fecundity of California fish was generally lower with respect to length and weight. The smallest number of developing eggs that Phillips found in the 1957-59 samples was 55.600 in a 324 mm TL fish (~30.5 cm FL). The largest number of developing eggs (915.200) was found in a 478 mm TL (~45 cm FL) female.

DISCUSSION

Geographical variation in age at maturity

Size at 50% maturity is apparently smaller in southern latitudes (Table 4); however, this may be due to factors other than geographic variation. Oregon and California fish differ only slightly in size after age 8 (Table 10) and the divergence in the growth rate only in younger fish is suspicious. Many fish sampled in California, especially the smaller fish, were sampled from the hook-and-line sport fishery, with 43 of the 134 immature fish landed commercially. The age-length discrepancy may be due to geographical variation, but possibly the larger of the immature fish move offshore where they are available to trawlers, the only catches sampled in Oregon. This possible movement of fish could cause the apparent increase in size at 50% maturity observed in Oregon.

Management implications (biological) based on maturity

The Oregon commercial fishery on widow rockfish in 1979-80 was almost entirely on mature fish. Therefore, the management question is how to best utilize mature fish. During this time there was no biological problem related to the catch of juvenile widow rockfish.

As long as there is not a fishery on juveniles, and as long as juveniles and adult stocks are separate, as apparently they are now, restrictions on size retained would seem to be inappropriate. Oregon female widow rockfish are 50% sexually mature at 38 cm FL, which could be used as a biological point of concern for Oregon fish. With the same reasoning, 33 cm could be the point of concern for California fish. However, since fecundity of small but mature females appears to be relatively low, a larger size may be more appropriate.

Table 10—Mean fork length and weight by sex at age for *Sebastes entomelas* from catches off Oregon and California.

	Mean length (cm)				Mean weight[1] (g)	
	Male		Female		Male	Female
Age (yr)	Ore.	Cal.	Ore.	Cal.	Ore.	
3	31.0	25.3	29.0	24.7	444	350
4	32.0	29.1	33.3	28.7	534	549
5	35.0	32.0	35.2	33.2	642	662
6	36.4	34.6	37.0	34.9	727	780
7	37.6	36.6	39.1	37.3	800	936
8	38.6	38.2	40.2	39.3	870	1,025
9	39.5	39.5	41.6	41.0	932	1.150
10	39.8	40.5	42.8	42.5	958	1.255
11	41.0	41.4	44.2	43.7	1.050	1.400
12	42.2	42.1	45.4	44.8	1.141	1.427
13	43.6	42.6	46.0	45.6	1.261	1.596
14	43.3	43.1	47.7	46.4	1.233	1.798
15	44.2	43.4	48.5	47.0	1.316	1,899
16	46.7	43.7	49.0	47.6	1.558	1.965
17	44.7	44.0	49.0	48.0	1.362	1.965
18	45.0	44.1	49.3	48.4	1.393	2,008
19	46.0	44.3	50.0	48.7	1.490	2.099
20	46.0	44.4	49.5	49.0	1.490	2,031
21	—	—	54.0	49.2	—	2,704
22	—	—	51.4	49.4	—	2.299
23	—	—	52.0	—	—	2.388

[1] Calculated mean weight, $w = a\,L^b$

Female: $a = 0.00545$; $b = 3.28781$; $r^2 = 0.99384$

Male: $a = 0.01188$; $b = 3.06631$; $r^2 = 0.99599$

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Appendix

Distribution (%) of mature widow rockfish by gonad condition and month in Oregon random market samples, 1979-80.

	Gonad Stage									
	Male					Female				
Month	3	4	5	6	7	3	4	5	6	7
January	0	0	0	19	81	61	39	0	0	0
February	0	0	0	2	98	1	11	70	5	3
March	0	0	0	0	100	0	3	22	48	27
April	0	0	0	0	100	0	0	0	0	100
May	0	0	0	0	100	0	0	0	0	100
June	100	0	0	0	0	0	0	0	0	100
July	83	0	0	0	17	0	0	0	0	100
August	0	100	0	0	0	0	0	0	0	100
September	9	91	0	0	0	21	0	0	0	79
October	10	90	0	0	0	100	0	0	0	0
November	0	98	2	0	0	100	0	0	0	0
December	0	36	37	27	0	98	2	0	0	0

First Pacific Symposium on Marine Sciences

The First Pacific Symposium on Marine Sciences was held in Nakhodka in the Primorsk region of the Soviet Union, August 7–16, 1986. The meeting was organized by the Scientific Committee on Marine Sciences of the Pacific Science Association (PSA), an international nongovernmental body devoted to initiating and promoting cooperation in solving scientific problems of the Pacific Basin. The committee is composed of three marine scientists from the Soviet Union, three from the United States, and one each from Canada, the Philippines, Japan, New Zealand, France, Tahiti, Australia, South Korea, and Indonesia. The American members of the committee are G. W. Boehlert (National Marine Fisheries Service (NMFS), Honolulu, Hawaii), J. C. Kelley (San Francisco State University, School of Science, San Francisco, Calif.), and G. R. Seckel (Pacific Fisheries Environmental Group, NMFS, Monterey, Calif.). The committee is chaired by V. I. Ilyichev, who is president of the Far Eastern Sciences Center of the U.S.S.R. Academy of Sciences and also the director of the Pacific Oceanological Institute in Vladivostok.

The topic of the meeting was "Matter and Energy Exchange in Water Mass, Ocean-Atmosphere, and Water-Bottom Sediment Systems and Their Impacts on Biota." After the arrival of the foreign participants on August 7, a tour of Nakhodka, and an opening address by Ilyichev, the program of scientific papers began on the afternoon of August 8 with an opening session with various papers on the El Niño–Southern Oscillation (ENSO) phenomenon, geochemistry, the Kuroshio-atmosphere interaction, and benthic "landscapes." The next day, 10 papers were presented in the first session, "Biological Productivity of the Ocean and its Determining Factors." Several of the papers combined biological and physical oceanography and covered topics such as the production system in the subarctic Pacific (C. B. Miller, Oregon State University, Corvallis), effects of interannual variation of currents on fisheries, including the Kuroshio (T. Sugimoto and M. Kobayashi, Ocean Research Institute, Tokyo) and the Tsugaru currents (K. Mizuno, Far Seas Fisheries Laboratory, Shimizu, Japan), and current-topography interactions and the effects on seamount productivity (Boehlert). Other interesting papers covered the variability and structure of frontal zones in the northwest Pacific (A. A. Malyshev and V. B. Darnitsky, Pacific Research Institute of Fisheries and Oceanography, Vladivostok) and the South Pacific (V. P. Pavlychev, Darnitsky, and I. A. Zhigalov, same institution).

The second session, "Short-Term Geochemical Processes and Their Impact on Ocean Bioproductivity," was highlighted by an experimental techniques paper on proton spin relaxation tomography applied to oceanography (U. K. Kopvillem, Quantum Oceanology Laboratory, Pacific Oceanological Institute, Vladivostok). Seven papers were presented in the third session, "Structure and Dynamics of Water Masses of the Biologically Active Zones in the Pacific Ocean." Notable among them were papers on vertical structure and internal waves at a shelf boundary (V. I. Ilyichev and V. V. Navrotsky, Pacific Oceanological Institute, Vladivostok) and an investigation of mid-latitude North Pacific winter wind systems (Seckel).

The languages of the meeting were Russian and English; simultaneous translations were provided. Most papers and sessions elicited considerable discussion. A formal round table discussion that was held the afternoon of August 10 covered means of fostering cooperation in marine sciences in the Pacific Basin. This included discussion by a wide variety of foreign participants, a statement of the goals and work of the PSA Scientific Committee on Marine Sciences by Ilyichev, and reports on the work of the following scientific institutes in Vladivostok by their respective directors: Institute of Marine Biology (A. V. Zhirmunsky), Pacific Institute of Research on Fisheries and Oceanography (TINRO; V. P. Pautov), Institute of Ocean Economics (V. A. Fedoseev), and Far Eastern Regional Institute of the State Committee on Hydrometeorology and Environmental Control (V. G. Fedorey). The discussions of this round table will be published in *Science in the U.S.S.R.*, a journal published in five languages and intended for a popular audience.

Two items of the planned work of the Scientific Committee on Marine Sciences, aside from the symposia, are of interest. First is the center for information exchange. Ilyichev has offered to support a center at the Pacific Oceanological Institute in Vladivostok to distribute scientific articles in the marine sciences. He proposes that individuals and institutions send copies of articles marked "for distribution" to the Pacific Oceanological Institute (7 Radio Street, Vladivostok 690032, U.S.S.R.). He will make an acquisitions list available, and anyone who submits articles may request any of the other articles on the list. There will also be extensive distribution to developing nations of the Pacific.

The second area of committee work involves multinational scientific expeditions. The first of these, involving Soviet, U.S., and Japanese scientists, began in June 1986 (for 120 days) on the Soviet research vessel *Academic A. Vinogradov*. This expedition will concentrate on geochemistry of mineral resources in the central Pacific. Although there is, as yet, no formal mechanism to form future expeditions, several were discussed informally by participants at the meeting and may be brought to the attention of the committee in the future.

In addition to the scientific session described above, a variety of informal discussions between scientists of the participating nations took place. The foreign participants spent August 11 visiting Vladivostok, a city that has generally been closed to foreign visitors. We toured the city, visited the Geological Institute, and met the director, S. A. Shcheka. On August 13, we arrived in Khabarovsk, where we met with scientists of five institutes of the Far Eastern Science Center.

Abstracts for many of the papers presented were distributed at the meeting. Full papers will be published in a separate volume by the Pacific Oceanological Institute and should be available early in 1987. Questions concerning further information on the meeting or specific papers may be directed to any of the four American participants:

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Plans for future symposia were considered at the final sessions. The committee decided that the symposia will be held in even-numbered years, between meetings of the Pacific Science Congresses and Intercongresses. The Second Pacific Symposium on Marine Sciences, to be held in the Soviet Union in 1988, will concentrate on marine resources of the Pacific Basin. The next Pacific Science Congress will be held from August 20–30, 1987, in Seoul, South Korea (note that the abstract deadline for the congress has been extended until early May). There are a variety of sessions of interest to oceanographers. Programs and the call for papers are available from the Secretariat, XVI Pacific Science Congress, KPP Box 1008, Seoul, Korea. The next Intercongress will be held in 1989 in Chile.

This report was contributed by George W. Boehlert, *Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Sevice, National Oceanic and Atmospheric Administration, Honolulu, Hawaii.*

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A REVIEW OF THE EFFECTS OF SEAMOUNTS ON BIOLOGICAL PROCESSES

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Abstract. Seamounts interacting with oceanic currents create flow complexities which depend upon current speed, stratification, latitude, and seamount morphology. Seamount effects, which include internal wave generation, eddy formation, local upwelling, and closed circulation patterns called Taylor columns, have important effects upon pelagic and benthic ecosystems over seamounts. The biological effects of these current-topography interactions are poorly understood. Flow acceleration on upper flanks of seamounts may lead to low sedimentation but areas of high standing stocks of benthic fauna, particularly filter feeders. Other effects extend into the water column; nutrient enrichment and enhanced primary productivity occur over some seamounts. Longer observational periods will be necessary to understand the time-varying nature of such enhanced productivity and the extent to which it remains at the seamount or is advected away. At higher trophic levels, unusual patterns of distribution and abundance occur at some seamounts. Maintenance of high standing stocks of seamount-associated micronekton and demersal fishes suggests that seamounts are locations for high rates of energy transfer. The energy driving this biological productivity may either be generated from in situ processes or be advected from elsewhere and concentrated at the seamount; interdisciplinary studies will be necessary to better understand these ecosystems.

Introduction

Seamounts represent a major physical feature of all ocean basins. For marine biota, they may be considered as islands separated by deep ocean areas; seamounts were thus the topic of many biogeographic studies [Wilson and Kaufman, 1987]. Biological communities at seamounts, however, may differ qualitatively and quantitatively from their continental shelf or slope counterparts at similar water depths [Hubbs, 1959]. In the open ocean, seamounts interact with ocean currents and create variability in the physical flow field. Several studies have described these effects on the Gulf Stream [Vastano and Warren, 1976] and the Kuroshio [Roden et al., 1982; Roden, 1987]. The physical effects include local small- and mesoscale phenomena including the shedding of mesoscale eddies which alter flow patterns for significant distances downstream of the seamounts [Royer, 1978]. Biological effects of these physical complexities are not well understood [Genin and Boehlert 1985; Boehlert, 1986]. Discovery of seamount fishery [Uchida and Tagami, 1984] and mineral resources [Manheim, 1986], however, has caused increased interest in seamount oceanography and its effects on biota [Darnitsky et al., 1984; Genin and Boehlert, 1985; Uchida et al., 1986].

The effects of sea floor topography on ocean currents have been a topic of interest to physical oceanographers for several decades. This area has recently been reviewed by Hogg [1980] and was the topic of a monograph by Kozlov [1983]. Semi-stationary eddies or Taylor columns above seamounts have been theoretically predicted and experimentally demonstrated in the laboratory [Taylor, 1917; Huppert and Bryan, 1976] and have been observed over some seamounts [Darnitsky, 1980; Owens and Hogg, 1980; Richardson, 1980]. Unfortunately, oceanographic surveys generally have station patterns inappropriate to detect these open-ocean, small-scale or mesoscale phenomena [Roden 1986]. Still, past theoretical and observational studies on the physics of topographic effects are available to serve as a background for biological studies.

Many studies have suggested that ecosystems at certain banks or seamounts are highly productive [Uda and Ishino 1958; Fedosova, 1974; Zaika and Kovalev, 1984; Tseitlin, 1985]. The ideas which explain such high productivity are typically based upon either local enhancement and subsequent

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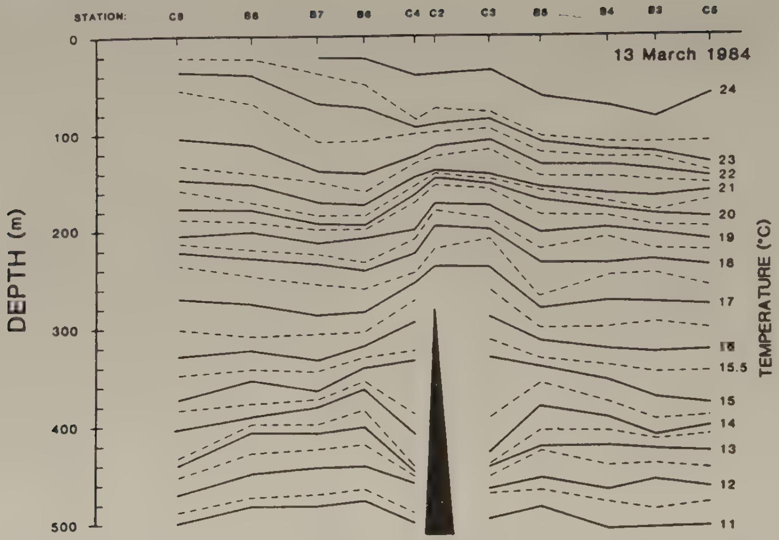

Fig. 1. Temperature structure at Minami-Kasuga Seamount (lat. 21°6'N, long. 143°8'E) along a west-east transect showing uplifted isotherms over the summit of the seamount. Note that the vertical scale is 50 times greater than the horizontal scale. (From Genin and Boehlert, 1985.)

retention of productivity or advection and concentration of food produced elsewhere. Some support exists for each of these hypotheses. Differences often exist between the pelagic ecosystems of waters above seamounts and adjacent, oceanic waters, including nutrient concentrations [Kozlov et al., 1982], chlorophyll [Genin and Boehlert, 1985], plankton biomass [Bezrukov and Natarov, 1976], ichthyoplankton [Nellen, 1973], and micronekton [Boehlert and Seki, 1984]. In the case of advected productivity, however, seamount populations may not be limited by local production, but rather by physical aggregation mechanisms [Isaacs and Schwartzlose, 1965; Darnitsky et al., 1984], which have been shown to exist in gyres and near reefs and coastal headlands [Alldredge and Hamner, 1980; Olson and Backus, 1985]. Benthic ecosystems on seamounts and islands may similarly differ from corresponding systems on continental shelves and slopes but have typically been less well studied. In many cases, unusual or even unique faunas exist [Simpson and Heydorn, 1965; Littler et al., 1986]. In addition, more recent studies have investigated the relationship of benthic fauna to current speeds and seamount-induced physical variability [Genin et al., 1986]. In this paper we review the effects of seamounts on biological processes, particularly as they affect pelagic and benthic ecosystems and fisheries productivity.

The Pelagic Ecosystem at Seamounts

Much of the impact of seamounts on pelagic ecosystems may be traced to current-topography interactions, which have been summarized in this volume by Roden [1987]. Where seamounts act as obstacles to current flow, compression of streamlines will occur due to flow acceleration. Local deflections of isotherms, usually in the form of uplifting, have been observed above several seamounts at different locations and depths [Meincke, 1971; Vastano and Warren, 1976]. Taylor columns represent an interesting phenomenon pertinent to seamounts; associated theory [Taylor, 1923; Huppert and Bryan, 1976] predicts such deflections as a result of the encounter between a current and a seamount. Under certain conditions of current, stratification, and topography, a closed streamlined anticyclonic vortex, or Taylor column, is expected to remain trapped above the seamount [Hogg, 1973; Huppert, 1975]. Such trapping may enhance nutrients shallower in the water column and if the residence time of a water mass above the seamount is sufficiently long, result in enhanced primary productivity and transfer into higher trophic levels. In this section we consider evidence for such enhancement and the role it plays in different trophic levels.

Nutrients and Primary Productivity

The uplifting of isotherms over seamounts is distinct and occurs with sufficient frequency to provide support for Taylor column dynamics. As an example, isotherms over Minami-Kasuga Seamount in the Mariana Archipelago [Genin and Boehlert, 1985] showed a clear uplift (Fig. 1) which did not reach the surface. Such upwelling at seamounts, like coastal upwelling, will transport nutrients into the euphotic zone where the primary production is nutrient-limited; an analogous situation exists around islands in stratified seas, where increased tidal mixing may stimulate primary productivity [Simpson et al., 1982]. Observations on a variety of seamounts support this contention; Bezrukov and Natarov [1976] suggested that vertical velocities on the order of 0.00003 to 0.0008 $cm \cdot sec^{-1}$ exist over various seamounts and that differences in the magnitude of upwelling may explain variability in seamount productivity. Vortices associated with seamounts can produce physical structures much like open-ocean cold core rings, except they remain centered over the seamount. Kozlov et al. [1982] describe a "columnar distribution" of temperature, salinity, silicate, and phosphate over one of the summits of Milwaukee Seamount in the southern Emperor Chain, in which elevated nutrient levels corresponding to the values at the seamount flanks reach high into the water column. Two visits, one month apart, to Pulkovskaya Seamount in the South Pacific suggested that vortices existed around the twin peaks and "satellite" vortices remained in surrounding waters. Again, signals were apparent in salinity, temperature, and silicate; silicate concentration at the summit depth of 500 m extended to the surface, with values nearly double that in surrounding waters [Kozlov et al., 1982]. Darnitsky et al. [1984] studied nutrients over Wanganella Bank near New Zealand during six visits from 1974 to 1977. Although upwelling and the resultant nutrient enrichment were clearly observed twice, the water was stratified with no apparent seamount effect during four other transects.

A shorter time scale was addressed in a study by Genin and Boehlert [1985], who conducted a series of transects to describe temperature and chlorophyll distribution over Minami-Kasuga Seamount. On the first of three surveys made within a month, uplifted isotherms formed a subsurface cold dome above the seamount (Fig. 1). The vertical displacement of the uplifted isotherms gradually decreased with distance above the seamount, from a 50 m uplift of the 17° isotherm close to the substratum, to a decay of the cold anomaly at about 80 m depth (180 m above the seamount top). Different deflection trends of isotherms in the vicinity of the substratum around the seamount slope formed a "boundary zone" comprising three distinctive layers composed of downward deflected isotherms from approximately 500 m to about 420 m, a relatively well mixed "transition zone" (Fig. 1) between the 14.5° and 15° isotherms (approximately 50 m above the previous layer), and an upwelling layer shallower than 340 m. These layers may be related to energy dissipation in the benthic boundary layer and agree with the statement by Bezrukov and Natarov [1976] that there is typically a change in the sign of vertical velocity between 300 and 600 m on the flanks of seamounts. On this first survey, calculations based upon seamount morphology suggested that conditions favoring maintenance of a Taylor column were present. Three chlorophyll profiles taken within the cold dome showed a distinctive maximum between 80 and 100 m depth, whereas the chlorophyll maximum layer at the four control stations was comparatively diffuse (Fig. 2). The causal relationships between the localized upwelling and the biological response are corroborated by the confinement of the chlorophyll increase to depths below 80 m, the uppermost edge of the cold dome. The chlorophyll concentrations at shallower depths above the seamount and at the control stations varied little throughout the area. These results clearly contrast with data from the second and third surveys in which neither cold dome nor chlorophyll increases were detectable along the same transects. These observations suggest that varying strength of oncoming currents result in a varying time scale for presence of the uplifted isotherms. Estimates of the time necessary for the formation of the observed chlorophyll maximum from the first survey, however, suggest a minimum residence time of the hypothesized Taylor column on the order of days [Genin and Boehlert, 1985].

The vertical extent and residence time of seamount-induced upwelling will determine the magnitude of its effect on local biological processes in overlying waters. Unfortunately, the temporal sampling scale of the studies described above is inadequate to determine the temporal dynamics clearly, and knowledge of regional currents is frequently lacking; moreover, the time scales will vary from seamount to seamount, which will have an effect on the manner in which any enhanced primary productivity may reach higher trophic levels. In oligotrophic oceans, phytoplankton production would increase if the uplifted isotherms penetrated into the euphotic zone, replenishing its depleted water with nutrients, as noted by Kozlov et al. [1982] and in the first survey by Genin and Boehlert [1985]. Entrapment on the order of days would probably affect only the primary producers, and hence, a patch of relatively high chlorophyll concentrations would be associated with the seamount. A longer residence time, on the order of several weeks, may locally affect the growth and abundance of zooplankton species; months would be necessary for micronekton [Pudyakov and Tseitlin, 1986]. Lagrangian current observations made above the Emperor Seamounts [Cheney et al., 1980] and the Corner Rise Seamounts [Richardson, 1980] suggested entrapment periods up to several weeks within seamount-generated anticyclonic eddies. Much longer periods (on the order of several months) were inferred from hydrographic and Eulerian current measurements above a deep seamount in the North Atlantic [Owens and Hogg, 1980]. If local enrichment persists for long periods and is a recurrent phenomenon, nektonic organisms may be attracted to or aggregated in these habitats [Uda and Ishino, 1958; Boehlert and Seki, 1984; Uchida and Tagami, 1984]. An analogy may be drawn to demersal plankton in nearshore reef systems [Hobson and Chess, 1978; Alldredge and King, 1985].

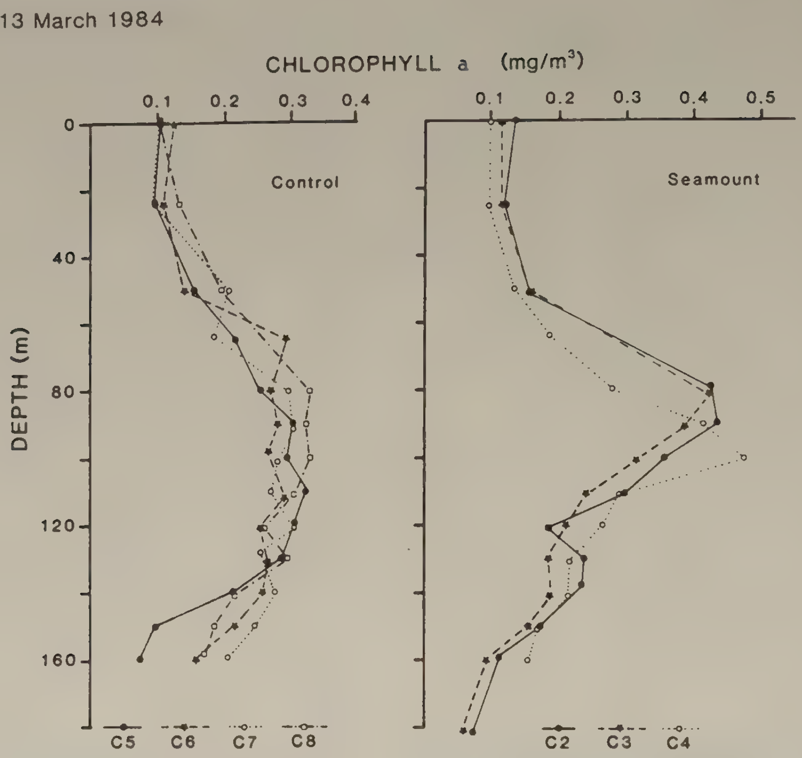

Fig. 2. Chlorophyll *a* profiles above Minami-Kasuga Seamount taken concurrently with the temperature transects shown in Figure 1. Three stations were occupied over the top of the seamount (right) and at control stations which were 10 km from the seamount summit (left). (From Genin and Boehlert 1985.)

Zooplankton and Nekton

Evidence concerning densities of planktonic organisms above seamounts is often conflicting. Sorokin and Sorokina [1985] noted no differences between waters above seamounts and surrounding waters with respect to bacterioplankton. Many surveys in the regions of seamounts, however, indicate two- to eightfold increases in zooplankton abundance in waters over seamounts [Fedosova 1974]; Zaika and Kovalev [1984] summarize results from a variety of Soviet papers. Zooplankton samples were taken by Genin and Boehlert [1985] in two of their three surveys, one during elevated and the other under normal chlorophyll levels. Zooplankton displacement volume was greater above the seamount only on the first survey; in contrast to the chlorophyll signal, however, zooplankton volumes were higher within the cold dome and above it, possibly indicative of the more vertically mobile nature of zooplankton [Genin and Boehlert 1985]. Whereas the studies referred to above have typically considered zooplankton biomass, it may be more appropriate to consider specific taxa, which may be either more abundant or relatively depleted in waters above seamounts [Hirota and Boehlert, 1985].

A specific component of the plankton studied above seamounts has been the ichthyoplankton. In the North Pacific, Borets and Sokolovsky [1978] observed no differences in ichthyoplankton abundance or species composition above seamounts as compared to distant waters; Belyanina [1985] had similar results in the Indian Ocean. Nellen [1973], however, in a study on the Great Meteor Seamount, noted increased abundance of neritic species and depletion of others, most typically midwater fish larvae, above the seamount. Boehlert [1985] described ichthyoplankton densities from winter and summer cruises at Southeast Hancock Seamount. Fish larvae at this open-ocean seamount are dominated by midwater rather than neritic species. In the summer, daytime samples showed no difference between the seamount and reference stations with the exception of the 50-100 m stratum (Fig. 3A). At night, however, the densities at the reference station were significantly increased as compared to daytime values, but not in the samples taken over the seamount. Samples taken on a winter cruise showed a different pattern from that in the summer (Fig. 3B); ichthyoplankton densities over the seamount were much greater than at the reference station, and the pattern held for night and day. These data

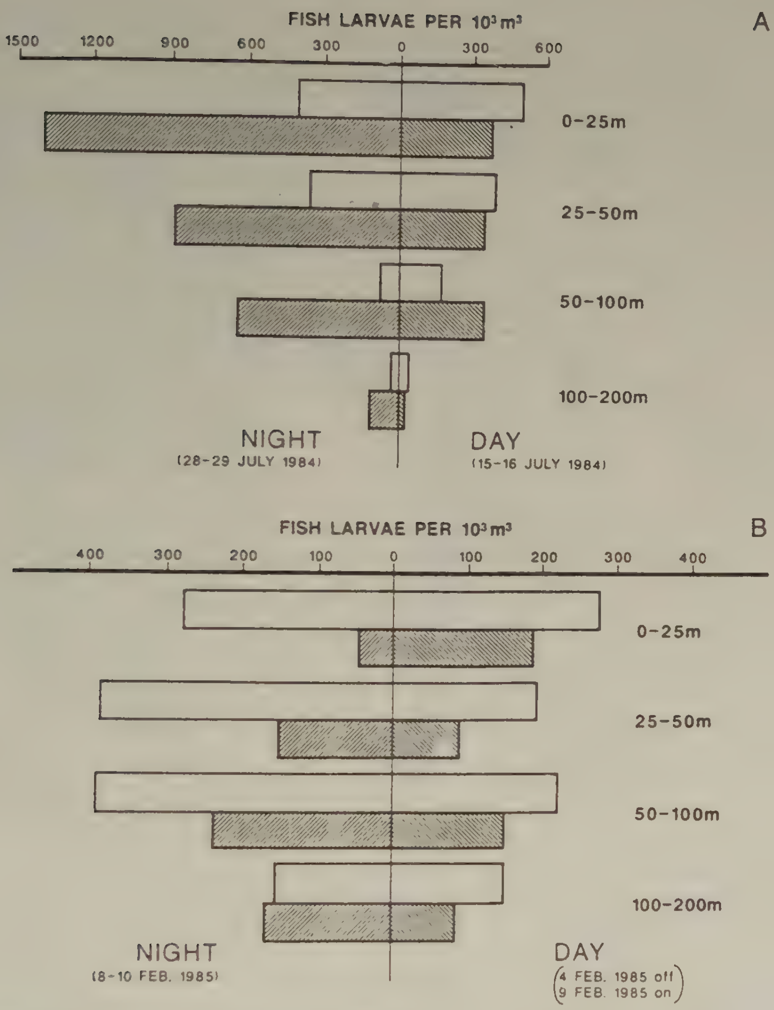

Fig. 3. Comparison of ichthyoplankton densities above Southeast Hancock Seamount (lat. 29°8'N, long. 178°5'E) with those at reference stations 20 km away. Samples were taken at discrete depths with an opening-closing Tucker trawl. A. Summer 1984. B. Winter 1985. Daytime densities are on the right, nighttime on the left, with each value the mean of duplicate samples. Densities above the seamount are represented by the upper (solid) bar, densities at the reference station by the lower (cross-hatched) bar. (Presented in Boehlert, 1985.)

suggest that some phenomena differing between winter and summer (or an aliased time scale) impact the abundance of these taxa.

As compared to the passive planktonic species, micronekton and nekton have more control over their movements. Fewer studies over seamounts have been conducted on these species, but Uda and Ishino [1958] suggested that aggregations of such animals may result in enhancement of fishing grounds. Densities may be estimated using hydroacoustic observations and net sampling. Some organisms normally rare in open-ocean areas may be abundant on seamounts. The sternoptychid fish, *Maurolicus muelleri*, typically associated with continental shelf-slope breaks, has been observed in abundance over South Atlantic and North Pacific seamounts [Linkowski, 1983; Boehlert and Seki, 1984]. Kozlov et al. [1982] noted vertical columns of scattering layers over two seamounts in the North Pacific but mistakenly considered them to be simply vertical manifestations of the oceanic scattering layers arrayed vertically like the "columnar" distributions of temperature and nutrients. Hydroacoustic observations at night above Southeast Hancock Seamount [Boehlert and Seki, 1984] showed pronounced scattering (Fig. 4).

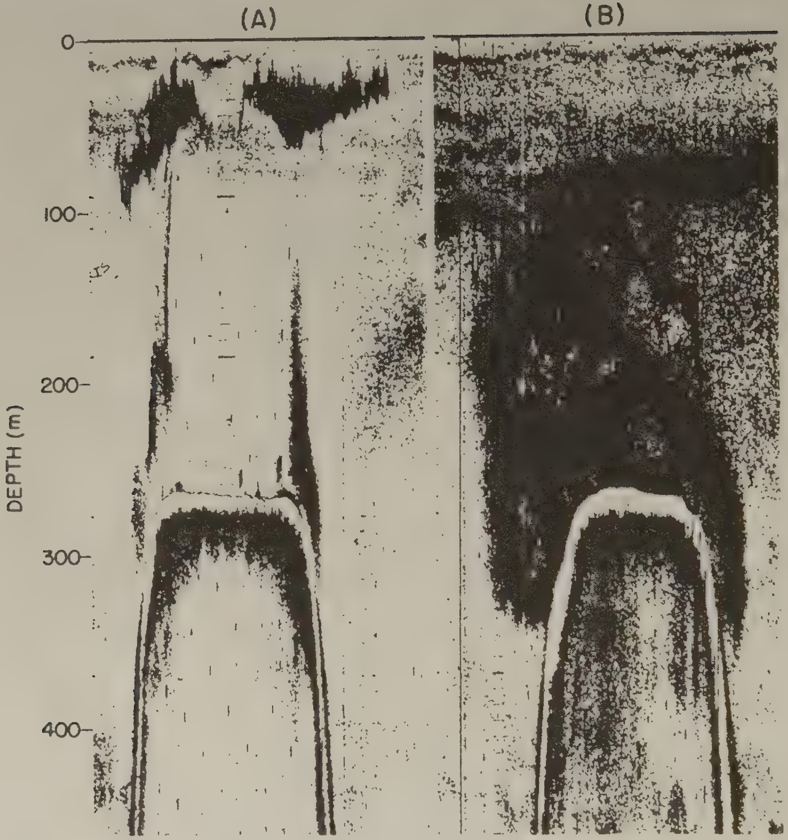

Fig. 4. Acoustic transects over Southeast Hancock Seamount on 17-18 July 1984 taken with a 38 kHz echo sounder. Each transect, from west to east (left to right) near the central axis of the seamount, took approximately 25 min. The distance across the flat portion of the seamount is approximately 1.8 km. A. 1931 h. Note the scattering layers rising off the seamount flanks to a depth of 40-60 m; net samples show these early layers to be predominantly Maurolicus muelleri. Sunset was at 1907. B. 0330 h. The layer has developed over the seamount extending from the flanks upwards to near 100 m; it developed this configuration at approximately 2130 and remained in a similar configuration throughout the night, until dispersing in early morning. These scattering targets may have been larger fishes or squids not sampled by our midwater trawl. (Presented in Boehlert and Seki, 1984.)

Scatterers typically remained on the flanks of the seamount by day, but began streaming vertically upward to depths near 50 m early in the evening (Fig. 4A), followed by consolidation of the shallow layers, a slight sinking of the top layer, and expansion downwards until the scattering layer extended from the summit of the seamount upwards to approximately 100 m depth (Fig. 4B). By contrast, no deep scattering layers in surrounding oceanic waters displayed either such high density or this type of behavior, suggesting that organisms specific to the region of the seamount were responsible for the acoustic traces. Subsequent hauls with midwater trawls demonstrated differences in abundance and species composition between waters above the seamount and at the reference stations. Maurolicus muelleri and the lophogastrid mysid, Gnathophausia longispina, dominated the catch over the seamounts. A third species, the sepiolid squid, Iridoteuthis iris, was characteristic of the deeper portions of the seamount scattering layer (Fig. 5A). In waters away from the seamount, oceanic taxa were generally more abundant and the three seamount taxa were either

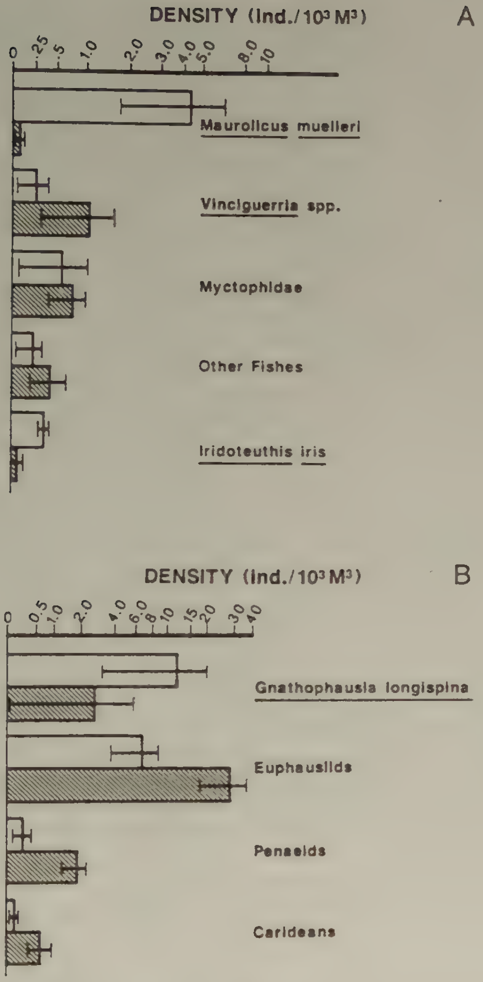

Fig. 5. Comparison of densities of selected micronekton taxa captured above Hancock Seamount with those taken at reference stations 5 to 20 km away in summer, 1984. Twelve samples were taken above the seamount and six at reference stations with a 6-ft Isaacs-Kidd midwater trawl, A. Fishes and squid. B. Crustacea. Two values are represented for each taxon; the upper (solid) bar indicates mean density (±2 S.E.) from the tows over the seamount while the lower (cross-hatched) bar indicates mean densities in off-seamount tows; note that abundances are on a log scale. (Presented in Boehlert and Seki 1984.)

absent or in low abundance (Fig. 5B). It would appear that this seamount, and others described above, have important effects upon the pelagic ecosystem. A better understanding of the local physical and biological oceanography will be necessary to determine the nature and cause of these effects.

Ecology of Seamount Benthos

Evidence that seamounts are inhabited by unique, and sometimes rich, benthic communities was first obtained in the surveys of Vema Seamount (South Atlantic) and Bowie and Cobb Seamounts (northeast Pacific), all shallow seamounts where scuba diving was used [Simpson and Heydorn, 1965; Scagel, 1970; Birkeland, 1971]. Developments in deep-sea photography allowed the first visual examination of deeper seamounts. Some of the first photographs [Heezen and Hollister, 1971] showed current-swept beds inhabited by corals, sea pens, anemones, sponges, crinoids, and other sessile suspension feeders on Eltanin Seamount (southeast Pacific, 162 m), Kelvin Seamounts (western North Atlantic, 1,419 m, 903 m), and Ampere Seamount (North Atlantic, 143 m, 529 m). Other studies have revealed dense populations of the gorgonian coral, Ellisella flagellum, seen in photographs taken on Josephine and Great Meteor Seamounts (east Atlantic, 200–300 m; Grasshoff, 1972] and the high abundance of sponges, hydroids, bryozoans, and serpulid tubeworms on the top of Patton Seamount (Gulf of Alaska, 433 m; Raymore, 1982].

Most of the photographic investigations noted above were rather limited in spatial coverage, with photographs taken at only a few locations on each seamount. Only with the use of more advanced photographic instruments could the distributional patterns of deep seamount benthos be studied. Genin et al. [1986] used the Deep Tow [Spiess and Tyce, 1973] and Grigg et al. [1987] used towed sleds to take hundreds of photographs along several transects on different parts of seamounts. Manned submersibles have also been used recently in seamount studies, allowing detailed surveys of megafauna as well as small meiofauna [Levin et al., 1986; Lissner and Dorsey, 1986]. Submersible investigations, which allow detailed observations and even experimental manipulations, hold great promise for understanding seamount benthos.

Seamounts are highly diverse habitats. A single seamount usually extends over a large depth interval, sometimes from the euphotic zone to the abyss. Substrata of seamounts vary from exposed rocky bottom to a continuous thick layer of sediments. The latter is usually found on the top of deep guyots and in topographic depressions, whereas rocky outcrops and extensive hard-bottom areas characterize the steep flanks as well as the tops of shallow guyots [Karig et al., 1970; Lonsdale et al., 1972; Raymore, 1982; Genin et al. 1986]. Sediments on seamounts can vary in grain size and can be rippled at one site and smooth at another. The sediment distribution pattern can be greatly affected by the topographically-induced current regime, creating sometimes a moat around the seamount base [Roberts et al., 1974]. Types of hard bottom on seamounts are highly variable, ranging from carbonate rocks and pillow basalt to rocks encrusted with a hard ferromanganese layer. Remarkably different substrata can even be found on a single seamount. In spite of this great variability, some unique environmental conditions seem to lead to common biological characteristics of seamount benthos. These features include the clarity of overlying waters and extended light penetration, the presence of deep rocky substratum, and the exposure to strong currents. The effects of these conditions on the structure of biological communities on seamounts are the focus of this section.

Shallow Seamounts--Effects of Water Clarity and Isolation

Far away from sources of terrigenous turbidity, mid-ocean seamounts (like many oceanic islands] are characterized by exceptionally clear overlying waters, where the attenuation of light is far lower than in coastal waters. Consequently, benthic autotrophs may occur in greater depths. The deepest known plant life, for example, has recently been discovered on San Salvador Seamount in the Bahamas, where an undescribed species of coralline alga was found at 268 m [Littler et al. 1986]. The flat top of this seamount contains a rich and exceptionally diverse multi-layer community of macroalgae with planar algal cover (understory and canopies) exceeding 100%. On Tanner and Cortes Banks (off southern California), a dominant macroalga, Eisenia arborea, grows as deep as 40 m, whereas its lower limit at coastal sites in the Southern California Bight is between 5 and 12 m depth [Lewbel et al., 1981; Lissner and Dorsey, 1986]. Macroalgal species on these and other banks exhibit similar depth extensions [Scagel, 1970; Lissner and Dorsey, 1986]. Most of these species are usually found in the lower intertidal or upper subtidal zones. This extension was also the case with some intertidal animals, such as the mussel, Mytilus californianus, found in relatively greater depths on Bowie Seamount [Scagel, 1970] and on a submerged pinnacle off the northwest coast of Washington [Paine, 1976]. Depth extensions of animals were attributed to biological factors, such as the rarity or absence of predators [Paine, 1976]. The asteroid, Pisaster ochraceus, determines the lower limit of Mytilus in coastal regions but is rare on the submerged pinnacle due to the lack of an intertidal zone. Small recruits of Pisaster are found primarily in the lower intertidal zone where they feed on small barnacles [Paine, 1976].

In addition to extensions of depth ranges, distinctive differences between animal communities on seamounts and those at adjacent coastal sites at corresponding depths have been described on several shallow seamounts [Birkeland, 1971; Lewbel et al., 1981]. Suspension feeders are typically in much greater abundance on Tanner and Cortes Banks than in corresponding coastal regions [Lewbel et al., 1981]. The scallop, Hinnites multirugosus, dominates the entire primary substratum on vertical surfaces of Cobb Seamount, whereas it exhibits a scattered distribution in coastal areas of the northeast Pacific [Birkeland 1971]. Tunicates, which frequently dominate rocky areas on the coasts of Washington, are represented by a single species on Cobb Seamount, and neither hydroids nor barnacles have been observed on the seamount. On the other hand, the community on Cobb Seamount differs from that on Bowie Seamount; barnacles and hydroids are found on the latter but not on the former, and different molluscs are dominant at each site. Such changes are probably caused by inter-site differences of ecological conditions combined with differences of colonization history. The presence of brooding species (the asteroid Leptasterias) and species with no planktonic larvae (the gastropod Searlesia dira) on Cobb Seamount [Birkeland, 1971] suggests that rare colonization events can affect the structure of the community on each seamount. Propagules of the brooding asteroids, for example, probably reached Cobb Seamount with drifting kelp [Birkeland, 1971].

Deep Seamounts--Effects of Substratum and Currents

The most distinctive characteristic of deep seamounts is the occurrence of extensive areas of hard substratum. Unfortunately, most information on the abundance of deep hard-bottom species on seamounts is incomplete, largely due to the small number of detailed surveys conducted. Furthermore, most of the observations were obtained with dredges or photography, so that very little is known about the abundance of smaller organisms. Large suspension feeders, including sponges, horny corals (gorgonians), black corals (antipatharians), ahermatypic scleractinian corals, anemones, tunicates, brisingid seastars, and crinoids, are the dominant taxa which have been observed. Their abundance generally decreases with depth [Grigg et al., 1987]. Photographs taken shallower than 1,000 m usually exhibit several taxa in each frame, sometimes forming dense communities (Fig. 6, and Heezen and Hollister, 1971; Grasshoff, 1972; Raymore, 1982; Genin et al., 1986]. Rich gorgonian fields occur on several seamounts (depth <1,000 m) in the Emperor Seamount chain (northwest Pacific). The discovery of these fields in the late 1970's caused a sharp decline in prices of precious corals on the world market [Grigg, 1984].

In oligotrophic oceans, even shallow seamounts, such as Cross Seamount near Hawaii (summit depth 300 m), exhibit sparse communities [Grigg et al. 1987], whereas relatively high densities of large suspension feeders are sometimes found in greater depths on seamounts located in fertile waters (e.g., on Kelvin Seamount at 1419 m depth; Heezen and Hollister, 1971]. In addition to the fertility of overlying waters, differences in the abundance of organisms on different seamounts can be related to local environmental conditions and to availability of sources of larvae (i.e., the presence of adult populations upstream of a sea-

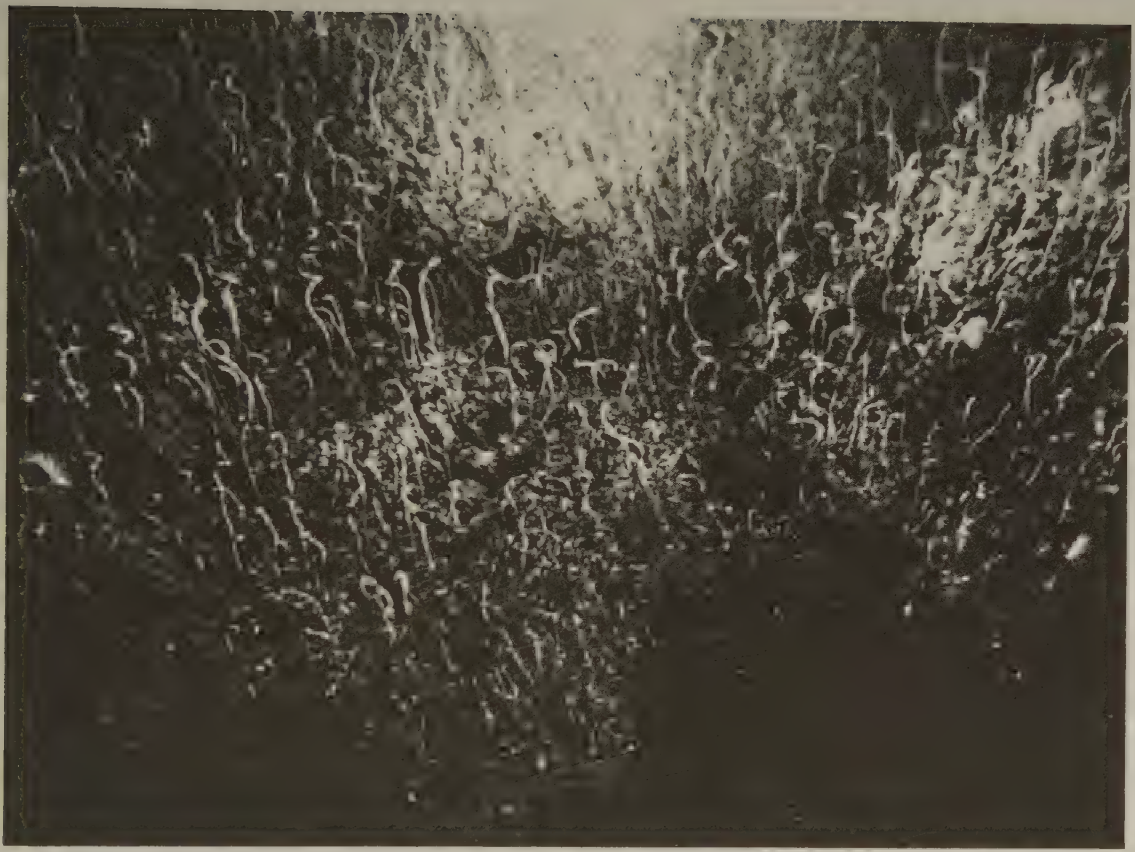

Fig. 6. Antipatharians, sponges, and other suspension feeders near a satellite peak at 700 m depth on Jasper Seamount in the northeast Pacific. Stichopathes sp., the whip-like black coral, is the most abundant megafaunal species between 600 and 1,000-m depth.

mount; Lutjeharms and Heydorn, 1981b; Grigg et al., 1987].

The presence of several satellite peaks on Jasper Seamount allowed Genin et al. [1986] to separate the effects of depth and topography on the abundance of animals. It was expected that passive suspension feeders would be generally more abundant at shallower depths, where the concentration of particulate food in the impinging waters is greater. The observations, however, showed that within a certain depth range the distance from a peak is a key factor in determining animal densities. The densities of a dominant species on Jasper Seamount, the black coral, Stichopathes sp., were significantly higher near peaks than in mid-slope areas at corresponding depths (Fig. 7). A similar increase in the densities of corals on the upper part of a slope, near a peak, has been observed at ca. 2,000 m depth on Horizon Guyot (central North Pacific, A. Genin and K. L. Smith, Jr., unpubl. manuscr., 1986). Other distributional patterns of large suspension feeders on seamounts further support the hypothesis that the abundance of animals on seamounts is determined by factors related to the local topography. These patterns can be separated into three spatial scales, namely patterns observed on the entire area of a seamount, patterns on topographic features such as knobs and pinnacles, and small-scale patterns such as those seen within a photograph. The large-scale patterns include the above-mentioned increased densities near peaks. They can be divided into patterns on narrow tapering peaks and those on wide or flat peaks. Densities on narrow peaks are greatest near the crest, whereas densities on flat tops of guyots and on gently sloping peaks are higher near the rim than near the center (Fig. 8 and Genin et al., 1986,

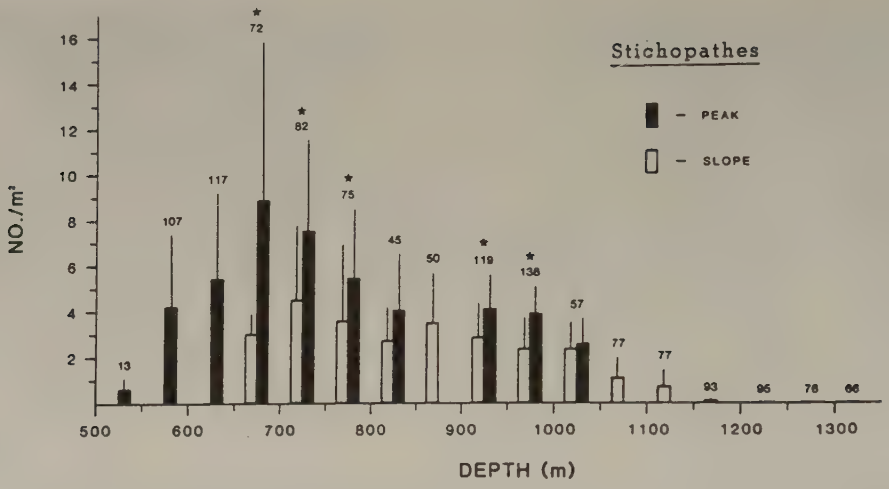

Fig. 7. Densities of Stichopathes (mean ± s.d.) at different depth intervals on Jasper Seamount. The photographs were divided into those near peaks (solid bars) and those >150 m below a peak (open bars). Stars indicate the intervals in which the mean near-peak density is significantly higher than the mean mid-slope density ($P < 0.001$, Mann-Whitney U test). The number of photographs taken at each depth interval is indicated above the corresponding bar. (From Genin et al., 1986.)

Jasper Seamount; Grigg et al., 1987, Cross Seamount). A similar increase of coral densities was observed along the rim of Fieberling Guyot (eastern North Pacific, ca. 500 m depth; A. Genin, unpubl. data). On the scales of tens of meters, animal densities are usually greater on topographic prominences, such as pinnacles and knobs, than in surrounding areas (e.g., Fig. 8). On the smaller scale, suspension feeders are frequently aggregated on upper parts of rocks, and small animals were found on protruding parts of larger organisms, such as sponges.

The occurrence of similar distributional patterns on different seamounts, combined with hydrodynamic theories and observations, suggests that a topographically induced current regime is a key factor in determining the abundance of suspension feeders on deep hard-bottom seamounts. Two different mechanisms may enhance currents near the edges of wide peaks. First, the flow of waters impinging on the flank may be upwelled above a seamount's top. Due to conservation of potential vorticity, an anticyclonic motion is induced, resulting in an accelerated flow on the left side of a seamount (looking downstream) and deceleration near the center and on the right [Huppert, 1975; Huppert and Bryan, 1976]. Alternating tidal flows would thereby cause intermittent acceleration periods near the edges and recurrent deceleration near the center of wide peaks and guyots. The other mechanism is related to the reflection of internal waves along a sloping bottom, where intensification of the flow occurs, especially for those waves with frequencies within an octave of a critical frequency defined by the bottom slope, stratification, and Coriolis parameter [Wunsch 1969; Eriksen, 1982, 1985]. Such an intensification is not expected to be distinctive on the flat or gently sloping areas at the center of guyots and wide peaks, where animal densities are low.

Existing physical theories do not predict the occurrence of stronger currents near a crest of a peak as compared with a mid-slope site at the same depth and on a similar slope angle. Hydrographic observations, however, suggest that the upwelling above such peaks is confined to the proximity of the crest and does not occur over mid-slope areas [Bezrukov and Natarov, 1976; Fukasawa and Nagata 1978; Genin and Boehlert, 1985; Roden and Taft 1985]. Short-term current measurements made by Genin et al. [1986] on Jasper Seamount also showed differences between a peak and a mid-slope site; the average current speed near a peak was about twice the mean speed recorded at a mid-slope site at the same depth. The mid- and small-scale increases of densities of suspension feeders on knobs, pinnacles, and on the top of protruding rocks can be similarly explained by an exposure to enhanced currents as these structures protrude to higher elevations above the bottom and are therefore exposed to more energetic zones of the benthic boundary layer [Butman, 1986; Grant and Madsen, 1986]. Even on such small-scale features, however, variability in colonization rates may be related to small-scale flow structure [Nowell and Jumars, 1984]. Genin et al. [1986] proposed two different mechanisms through which intensified currents can induce higher animal densities. In the "settlement pathway," a site is colonized by relatively more recruits simply because more

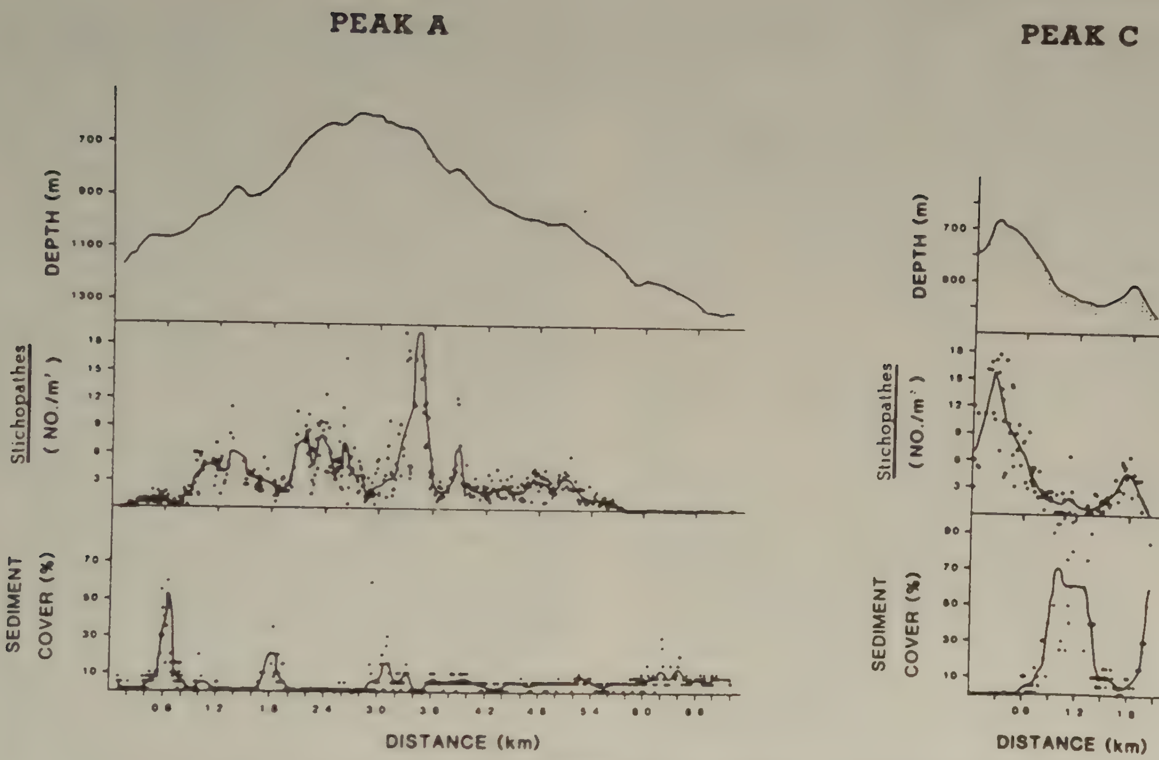

Fig. 8. Bathymetry, densities of Stichopathes, and sediment cover across two satellite peaks on Jasper Seamount. Each dot indicates the animal density or sediment cover in a single photograph. Solid lines indicate 9-point running means. Note that the animal densities follow the bathymetric line on the sharp peak (C) whereas lower densities are found near the center of the wide peak (A) than near its edges. Animal densities are relatively higher on small topographic prominences such as those at 1.4 and 3.9 km along the transect. Note the sharp increase of sediment cover in the topographic depression near peak C. (From Genin et al., 1986.)

water, and thereby more larvae, flow through per unit of time; in the "feeding pathway," more water flows past suspension feeders at sites characterized by stronger currents, resulting in increased feeding and growth rates and possibly higher survival rates of small recruits. The actual mechanisms involved are yet to be experimentally tested.

Very little is known about soft-bottom fauna on deep seamounts. Unlike hard-bottom epifauna, infauna in sedimentary substrata cannot be observed by photography. In a recent study of deep (1,000 to 3,000 m) seamounts in the Pacific Ocean off Mexico, Levin et al. [1986] used a submersible to investigate the effects of giant protozoans (xenophyophores) on local soft-bottom communities. Xenophyophores are abundant on seamounts where they agglutinate sediments to form large tests (up to 25 cm diameter) which protrude above the sediment. Sediments immediately surrounding these organisms exhibit higher densities and diversities of metazoan species relative to control sediments collected at distances of 1 m from those protozoans. Levin et al. [1986] propose that xenophyophores contribute to maintenance of high benthic diversity by altering hydrodynamic conditions and by providing metazoans with substratum, food, and refuge. The diversity of soft-bottom habitats on seamounts has not been compared with the surrounding deep sea; this would make an interesting investigation from a submersible, since a wide depth range occurs at a single site on soft-bottom seamounts.

The Role of Seamounts in Fisheries Productivity

Seamounts and banks may aggregate resident demersal and transient, pelagic organisms which can support fisheries [Uda and Ishino, 1958; Uchida et al., 1986]. Polovina [1985] compared seamounts with bank and island systems and found higher densities of the same species on the seamounts. A variety of demersal resources in high

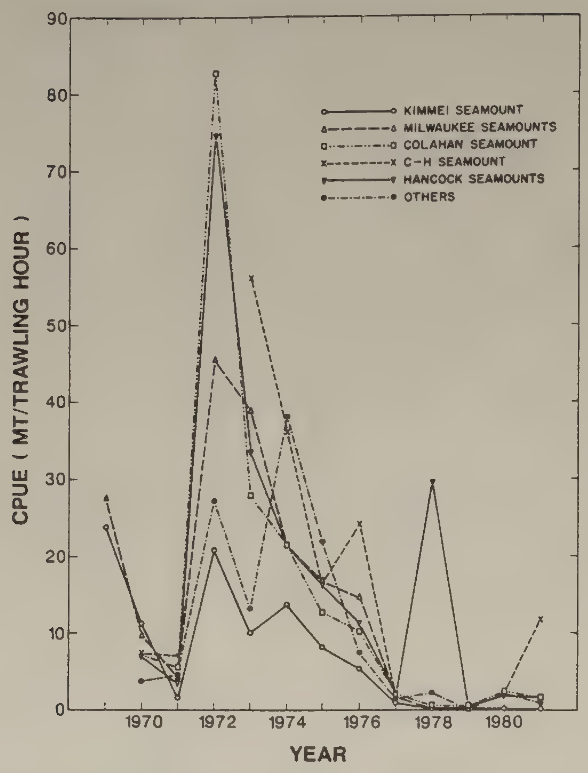

Fig. 9. Annual data on catch-per-unit-effort (an index of abundance) of Japanese trawlers for pelagic armorhead on several of the southern Emperor-northern Hawaiian Ridge seamounts, 1969-81. These data show the sharp decline in stock abundance. The Japanese catch was about one-fifth that of the Soviets; combined, they took approximately one million metric tons of this species off these seamounts during this period. (From Wetherall and Yong, 1986.)

abundance has been noted on seamounts including fishes [Sasaki, 1986], lobsters [Lutjeharms and Heydorn, 1981a], crabs [Hughes, 1981; Alton, 1986] and precious corals [Grigg, 1986; Genin et al. 1986]. Pelagic species such as tunas and squid may seasonally feed in waters above seamounts [Inoue, 1983; Yasui, 1986], as do some marine mammals [Hui, 1985]. In the open ocean, seamounts thus function as sites of increased production or aggregation of higher trophic level organisms.

A specific example of high fisheries productivity is provided in the southern Emperor and northern Hawaiian Ridge seamounts. Between 1967 and 1975, nearly one million metric tons of pelagic armorhead, Pseudopentaceros wheeleri, were taken by Soviet and Japanese trawlers, and standing stocks were estimated at nearly 400,000 metric tons [Borets, 1975; Sasaki, 1986]. Japanese data on catch per unit effort (Fig. 9) demonstrate extremely high catch rates which declined drastically in later years of the fishery. Some of the same physical mechanisms which alter the patterns of distribution and abundance of the taxa as described earlier for Hancock Seamount may be invoked to explain the availability of the energy necessary to maintain high densities of fish here and at other seamounts. First, convergent flow resulting in accumulation and greater flux of oceanic plankton and micronekton may provide prey [Isaacs and Schwartzlose, 1965; Darnitsky et al. 1984; Tseitlin, 1985]. Secondly, as described earlier, locally enhanced productivity may be retained in the region of the seamount. A Taylor column or other stationary water mass could retain this productivity, but the residence times of such features are unknown. Energy for the high biomass demersal fish resources, however, appears to be derived from oceanic rather than seamount-derived sources. This assertion is supported by diet studies of pelagic armorhead [Fedosova, 1976], species on seamounts in the Indian Ocean [Parin and Prutko, 1985], and elsewhere [Kashkin, 1984]. Simulation models of seamount fish populations [Tseitlin, 1985; Pudyakov and Tseitlin, 1986] suggest that such allochthonous energy inputs are necessary for population maintenance.

An intriguing question about these animal resources, given that most have pelagic larvae, is the mechanism of recruitment back to the seamount. One of the first suggestions of such a mechanism invoked the concept of stationary Taylor columns over seamounts for maintenance of pelagic larvae [Shomura and Barkley 1980]. This hypothesis is an extension of the ideas on the conservation of insular plankton described by Boden [1952]. Maintenance of pelagic larvae in closed circulations above large bank systems has recently been demonstrated in several locations [Dooley 1984; Sundby, 1984; Smith and Morse, 1985]. Others have suggested that seamount populations are derived from upstream source populations; the distances proposed have been as great as 1,100 nmi [Lutjeharms and Heydorn, 1981b]. In either of these cases, however, physical variability can lead to interannual variability in recruitment strength; such fluctuations may be characteristic of seamount resources [Lutjeharms and Heydorn 1981a; Wetherall and Yong, 1986]. Given the small geographic extent of seamounts and the variability in recruitment, great care must be taken to manage seamount resources and prevent overexploitation [Boehlert, 1986; Sasaki, 1986].

Conclusions and Suggestions for Future Research

As we have described in this paper, seamounts are sites where physical perturbations result in development of unique ecosystems. Understanding variability in the biological productivity of seamounts is a challenging research problem which will require interdisciplinary research. Mesoscale physical oceanographic studies will be necessary to define the conditions for development of eddies, Taylor columns, and other features of flow complexity. Small-scale studies of upwelling, turbulent mixing, and benthic boundary layer effects will better characterize the local conditions near the seamount. Concurrent studies of biological oceanography of the water column over seamounts can define the variability of nutrients and primary productivity and their residence times. By understanding the seasonal and interannual variability of these phenomena, we should be able to better define the importance of enhanced productivity to higher trophic levels and to determine the role of currents in concentrating or increasing the flux of allochthonous energy sources. In addition to these temporal components of variability, comparative studies of seamounts can provide an understanding of spatial variability. Given information on bottom topography and ocean currents, perhaps we can develop generalities or predictive capabilities concerning seamount productivity. In this comparative vein, we should consider other topographic features, including banks, coastal headlands, and islands, where related phenomena may occur.

Benthic communities on seamounts may provide an initial indication of productivity, since the benthos may serve as an integrator of productivity of the overlying water column; sediments, where they occur on or around seamounts, may provide a historical record of the patterns of such productivity. Most studies of seamount benthos, however, have been observational or descriptive. A greater understanding of factors structuring the communities on deep seamounts will undoubtedly require the use of submersibles. The remarkable changes of environmental conditions over relatively small distances on seamounts, combined with manipulative capabilities of research submersibles, could prove most useful in conducting controlled experiments to define the mechanisms which structure deep-sea communities.

Finally, the local modification of physical and biological conditions by mid-ocean seamounts provides a unique opportunity in marine research. Experimental manipulations commonly performed in marine intertidal and subtidal research have significantly contributed to the understanding of key ecological processes. Such manipulations cannot typically be performed on scales large enough to be applicable to the open ocean. Warm- and cold-core rings have provided natural experiments in which isolated pelagic populations have been studied [Backus et al., 1981; Olson and Backus, 1985]. Seamount-induced upwelling and eddy generation may provide similar "manipulations." Processes related to the formation and maintenance of the deep chlorophyll maximum, for example, may be studied with the temporally varying upwelling induced by seamounts. In addition, relationships between different time scales of physical events and the associated biological response at different trophic levels can contribute significantly to our understanding of marine ecosystems.

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Recruitment Dynamics of Metamorphosing English sole, *Parophorys vetulus*, to Yaquina Bay, Oregon

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English sole, *Parophrys vetulus*, spawn in shelf waters off the west coast of North America and early development occurs in coastal waters. Near metamorphosis, however, larvae recruit to nearshore and estuarine nursery areas, an uncommon life-history feature for a species in this region. Recruitment of larval *P. vetulus* to Yaquina Bay, Oregon, was sampled with moored nets on a weekly basis. Recruitment began during night flood tides in late February and was characterized by three peaks during the season. Planktonic recruitment continued into June, whereas benthic juveniles began to emigrate from the estuary in late May.

The data suggest that two developmental stages of recruits immigrated to Yaquina Bay. The first are newly transforming larvae which enter the bay earliest within each peak of recruitment; peaks of abundance are related to onshore Ekman transport. This transport also brings larvae to shallow areas along the open coast where they settle. These transforming stages are still capable of pelagic swimming activity and continue to recruit to the estuary, typically swimming deeper in the water column than the early stages. Estuarine factors, particularly bottom salinity at the end of ebb tide, are most strongly correlated with recruitment of these stages. It seems that tidal stream transport is the primary mechanism used by English sole to recruit to the estuary, but the mechanism of locating the estuary and timing of entry is relatively complex.

Introduction

Shallow-water estuarine nursery areas are important to the young of many fish and shellfish species; as many as 50–70% of the commercially exploited species of fishes in the western Atlantic, for example, utilize estuarine nursery habitats (McHugh, 1967; Clark *et al.*, 1969). The reasons for estuarine residence by young stages of predominantly offshore species include increased food availability and decreased predation rates (McHugh, 1967; Rosenberg, 1982). Many of these species spawn in offshore waters, where egg and early larval stages may be dependent upon prevailing current patterns for transport to nearshore areas (Nelson *et al.*, 1977; Miller *et al.*, 1984). The mechanism by which larvae locate and enter estuaries, however, is unknown. The high densities of larvae and juveniles

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within estuaries suggest that the mechanism requires active behavioural orientation by the larvae to specific characteristics of the estuaries, including salinity, tidal flushing and olfactory cues (Creutzberg, 1961; Creutzberg *et al.*, 1978; McCleave & Kleckner, 1982).

Only 10–20% of the Pacific coast is estuarine, as compared to 80% of the Atlantic and Gulf coasts (Emery, 1967). Thus, although estuarine utilization is more limited for Pacific than Atlantic coast fishes (McHugh, 1967; Pearcy & Myers, 1974), the problem of estuarine entry may be particularly acute for Pacific coast fishes whose young inhabit these nursery areas. Pacific estuaries are important to several fish species, including Pacific herring, *Clupea harengus pallasi*, which migrate to, and spawn in, estuaries (Rounsefell, 1930), and anadromous salmon which utilize estuaries as nurseries during their migration to the sea (Healey, 1980). Few offshore Pacific species, however, use estuaries as nurseries after metamorphosis (McHugh, 1967). Pearcy and Myers (1974) and Krygier and Pearcy (1986) concluded that Yaquina Bay, Oregon, was an important nursery area for several flatfish species that spawn offshore, because newly metamorphosed juveniles moved into the estuary in large numbers. The dominant species of juvenile flatfish in Yaquina Bay is the English sole, *Parophrys vetulus*.

The spawning season for *P. vetulus* is extended and annually variable, with peak spawning occurring as early as September and as late as April (Laroche & Richardson, 1979; Kruse & Tyler, 1983). Larvae hatch from pelagic eggs in 3–12 days, depending upon temperature (Alderdice & Forrester, 1968), and are the dominant species in the winter–early spring ichthyoplankton assemblage which occurs from nearshore to approximately 28 km seaward (Richardson & Pearcy, 1977; Mundy, 1984). Metamorphosis begins at approximately 16–18 mm and is complete by 20–22 mm SL (Ahlstrom & Moser, 1975; Rosenberg & Laroche, 1982); these lengths correspond to ages of approximately 70–100 days (Rosenberg, 1982), and recruitment to estuaries occurs at this stage (Misitano, 1976). It was previously believed that 0-group juveniles inhabited only estuaries and shallow protected inland coastal areas (Ketchen, 1956; Olson & Pratt, 1973). More recent sampling off the Oregon coast has shown the presence of populations in 15–50 m of water off the open coast as well (Laroche & Holton, 1979; Krygier & Pearcy, 1986). In the offshore area, newly settled juveniles are present from October to July; in Yaquina Bay they first appear in November and are last captured in June (Krygier & Pearcy, 1986). Peak immigration to Yaquina Bay apparently occurs from mid-January to late May, but may vary from year to year with timing of spawning.

Estuaries and shallow coastal areas appear to be important nurseries for *P. vetulus*, but the mechanism of recruitment to estuaries is not understood (Rogers, 1985; Krygier & Pearcy, 1986). Species with larval distributions offshore must first reach nearshore waters. Peterson *et al.* (1979) proposed a mechanism by which copepod populations could be maintained in the coastal zone despite offshore transport associated with upwelling. The recruitment season for *P. vetulus*, however, occurs prior to the upwelling season off Oregon, when onshore convergence is prevalent. The situation may thus be more similar to that for larval Atlantic menhaden, *Brevoortia tyrannus*, which are estuarine-dependent and apparently use onshore transport to reach estuaries (Nelson *et al.*, 1977).

In this paper, we present the results from a field study of temporal patterns of English sole recruitment to Yaquina Bay. However, rather than taking an approach concerned with interannual variability (Nelson *et al.*, 1977; Bailey, 1981), a finer temporal scale within a single year was considered. The relationship of estuarine entry to two types of environmental factors is described; the first type is offshore factors such as onshore Ekman transport, concerned with transport of larvae to the nearshore. The second group is

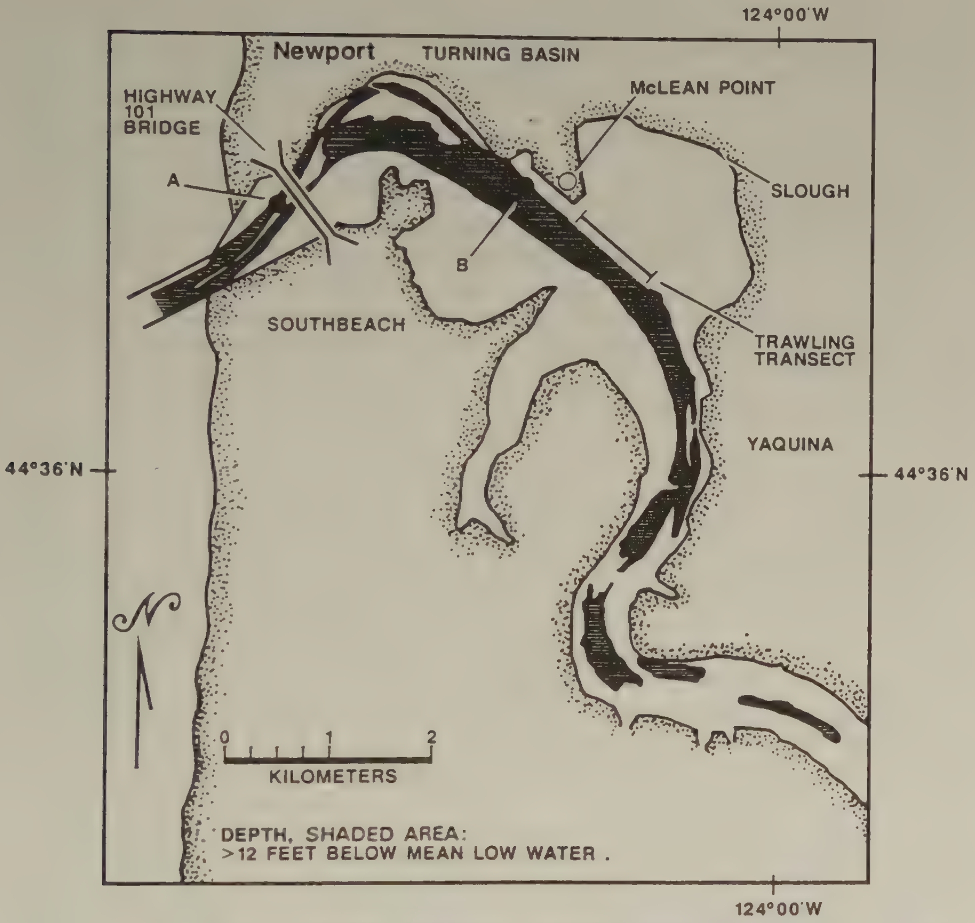
124°00'W
Newport
TURNING BASIN
McLEAN POINT
HIGHWAY 101 BRIDGE
A
SLOUGH
B
SOUTHBEACH
TRAWLING TRANSECT
YAQUINA
44°36'N
44°36'N
0
1
2
KILOMETERS
DEPTH, SHADED AREA:
>12 FEET BELOW MEAN LOW WATER .
124°00'W

Figure 1. Yaquina Bay, Oregon, site of sampling for early stage *Parophrys vetulus*. Prior to 23 February, samples were taken west of the bridge (A), but after that date were at point B after excessive current caused repeated anchor failure. Shaded areas in the bay indicate 3·16 m below mean low water.

associated with estuarine entry and includes river discharge, temperature and salinity differences, lunar phase and tidal currents. We discuss the relationship of the estuarine and offshore juvenile populations of English sole.

Materials and methods

Study area

Yaquina Bay, Oregon (44°36'N, 124°00'W) is a small estuary with an area of 11·6 km^2 (Figure 1). Sloughs and the river channel comprise 65% of this area; the remainder is tidelands (Percy *et al.*, 1974). The channel is maintained by dredging to a depth of 9 m from the narrow entry, between two breakwaters, to the ship turning basin at McLean Point (Figure 1), approximately 5 km from the mouth. Upriver of McLean Point, the channel depth is 3·6 m. Average monthly river discharge at Newport is 36 $m^3 s^{-1}$ with an average low near 2 $m^3 s^{-1}$ in August and an average high near 70 $m^3 s^{-1}$ in December–January (U.S. Army Corps of Engineers, 1970). Mixed semidiurnal tides with a tidal range of 1·7 m occur in the bay (Kulm & Byrne, 1967); flushing times are approximately 13·3 tidal cycles in the summer and the exchange ratio is 52% (Zimmerman, 1972). The estuary is partially mixed from November to May and well mixed from June to October (Burt & McAlister, 1959; Kulm, 1965). Temperatures in Yaquina Bay range from about 7 to 17 °C. Lowest temperatures occur in January and February, and the highest (but most variable) temperatures occur in summer, when high temperatures produced by local warming alternate on a tidal basis with cold, upwelled water from offshore (Bourke, 1969; Frolander *et al.*, 1973). Salinity depends upon freshwater input and reflects the ocean salinity from June to October in the lower bay; values are lower and more variable in the months of high freshwater runoff (Frolander *et al.*, 1973). Dissolved oxygen does not vary markedly with depth in the lower bay (W. DeBen, U.S. Environmental Protection Agency, Newport, OR 97365, unpubl. data).

Larval collections

Weekly collections of larval and juvenile *P. vetulus* were made from the 11-m RV *Sacajawea* on night flood tides from 14 January to 23 July 1982. Pelagic larvae were collected with moored nets (0·5-m mouth diameter, 0·75 mm mesh) modified from Graham (1972) as described by Weinstein *et al.* (1980). The nets were attached by pivots to aluminium collars and orienting vanes bolted to a nylon rope (1·25-cm diameter) suspended from a buoy. The line was attached to a 41-kg cement block shackled to a chain with a 9·1-kg anchor; a tag line and float on the anchor were used for retrieval. Three nets were set on each string, at 1·5 m below the surface, halfway between the surface and bottom, and 1 m above the bottom. The volumes of water filtered were measured with calibrated General Oceanics model 2030-R2 (large-rotor) flowmeters mounted in the centers of the net frames. Nets were set after slack low water and fished for 0·6–4·4 h, with the fishing time being dependent on the current velocity. Two strings of nets were initially set west of the bridge on the north side of the boat channel (Figure 1, Site A). Strong currents over hard substrates at these sites occasionally caused the nets to move. After 23 February, the sampling locations were moved farther into the estuary (Figure 1, Site B), to avoid movement of the nets and boat traffic. However, English sole larvae did not enter the bay in large numbers until about 3 March, so the change in location did not bias the catches. Furthermore, the two sites are similar in plankton composition because of high tidal exchange in the bay (Frolander *et al.*, 1973). Additional samples were taken to assess the abundance patterns of larvae by setting the anchored nets on both ebb and flood tides over 24-h periods on 17–18 March and 9–10 April 1982.

Detritus, mostly of terrestrial origin, occasionally clogged the nets and fouled the flowmeters. These problems were most severe in the bottom nets. Samples containing more than 4 l of total sample volume (including detritus), or in which the ratio of sample volume (l) to water volume filtered (m^3) exceeded 0·03 were discarded due to net clogging and excluded from further analysis. When flowmeter readings were missing due to fouling or other problems, filtered water volumes were estimated. Linear regressions were calculated from samples with reliable readings to estimate flowmeter readings from each net based upon readings from other nets on the same string. Only nine readings were estimated in this manner.

Demersal English sole were collected with a 1·5 m wide beam trawl (Kuipers, 1975) equipped with a 1-m diameter odometer wheel (Krygier & Pearcy, 1986) and a net with

1·6 mm bar mesh liner. Four replicate 5-min tows were taken while the anchored nets fished, except on dates when concurrent Tucker trawl samples were taken (9 April and 27 May); on those dates, beam trawl samples were taken within 48 h of the plankton samples. All trawl samples were taken on a transect south of a large slough, along the north edge of the boat channel at a depth of 4·5–8·0 m (depending on tidal stage) from a point opposite buoy 14 to the east edge of McLean Point (Figure 1). All tows were taken at night against the flooding tide. When fish were highly abundant (>5 per 10 m^2), density estimates were made from a single haul because our data showed little intersample variability in density, as noted by Krygier and Pearcy (1986). When fish were moderately abundant ($\geq 1{\cdot}5$, $\leqslant 5$ per 10 m^2), estimates were made from two samples.

Pelagic larvae were also collected with a 1 × 1 m Tucker trawl (Clarke, 1969) with an effective mouth area of 0·71 m^2 when fished at an angle of 45° (Boehlert *et al.*, 1985). The trawl consisted of three nets and a double-release mechanism operated with messengers; each net was 5 m long with 0·505-mm mesh and an effective open-area : mouth-area ratio of 6 : 1. The filtered water volumes were measured with calibrated General Oceanics model 2030 flowmeters mounted in the center of each net. A wire angle of 45° was maintained during each tow, and depths of tow were maintained by adjusting the amount of wire let out by predetermined amounts for each depth. Tucker trawl tows were made against the prevailing tidal current through the center of the boat channel and turning basin from approximately 400 m east of the bridge to the east edge of the turning basin (Figure 1). For each sample set, the water column was divided into three equal strata and 10-min oblique tows were taken throughout the surface, midwater and bottom strata. Duplicate samples were taken at each depth during flood, ebb, and on slack tides during the diel sampling on 9–10 April 1982, and during night flood/ebb tide comparisons on 20–22 and 27–28 May 1982. Additional single samples at each depth were taken during day flood and ebb tides without concurrent moored net samples on 4 May 1982.

All samples were preserved in the field with 10% formalin in seawater buffered with sodium borate. *Parophrys* larvae larger than 10 mm were sorted from the samples. Standard lengths of larvae were measured to the nearest 0·1 mm and lengths of juveniles (>22 mm SL) to the nearest 1·0 mm with dial calipers following the method of Laroche and Richardson (1979). Larvae were classified by developmental stages A–F using criteria modified from Tsuruta (1978). These stages are based upon the stage of metamorphosis and not on length, because transforming larvae were observed in early stages between 15·3 and 23·0 mm SL. The modifications from Tsuruta include a slightly different definition of stage F and an additional juvenile stage. The stage F used in this work includes fish in which the left eye has reached its final position, but the snout is not yet elongate and the lateral line had not begun to form; also, the left eye is once again visible from the left side. The additional juvenile stage of *Parophrys* includes those fish in which the lateral line has begun to form and the snout has begun to elongate, with the snout appearing pointed rather than rounded.

Observations of the duration of the stages were taken between 20 March and 9 April 1984. Thirteen *Parophrys* in early stage C were collected with the beam trawl on 20 March. They were maintained in a tank with a flow-through system using filtered water from the bay with ambient temperatures (10·4–14·0 °C) and salinities from 28–30·3‰. The fish were fed a mixture of *Brachionus*, *Tigriopus*, and *Artemia* nauplii *ad libitum* daily. Daily observations were made of stages and single fish were preserved every other day.

Surface and bottom temperatures and salinities were taken at the beginning and end of each anchored net set. Salinity samples were analysed with a Guildline Autosalinometer model 8400. Water depth was measured at the moored net stations at the beginning and end of sampling. Tidal heights, maximum current velocities, time of maximum and minimum currents, time of high and low water, and lunar phase were obtained from tide and tidal current tables (National Ocean Survey, 1981*a,b*). Daily mean values of Yaquina River discharge ($m^3 s^{-1}$) were obtained from C. G. Kroll (United States Department of the Interior Geological Survey, Water Resources Division, Pers. comm., 31 August 1982). Weekly values of the coastal divergence (upwelling) index were provided by A. Bakun (Pacific Fisheries Environmental Group, National Marine Fisheries Service, NOAA, Monterey, CA 93942). Six-hour estimates of adjusted sea level, related to alongshore water transport (Marthaler, 1977) were provided by A. Huyer (Oregon State University, College of Oceanography).

Results

Gear comparison

Catches of the moored nets and Tucker trawl were compared to determine if avoidance of the moored nets occurred. Too few larval *Parophrys* were taken in daytime samples by either gear to determine if avoidance was greater for the moored nets during daylight. In night samples, however, no significant difference was found between the mean catches of the moored nets and Tucker trawl in paired samples at each depth on each tide (t-test; d.f.$=23$; $p<0{\cdot}05$) or in the mean lengths of larvae in those samples (t-test; d.f.$=28$; $p<0{\cdot}05$). Avoidance of the moored gear relative to the towed nets was thus not observed, which is similar to results of gear comparisons for larvae and juveniles of other species of estuarine fishes (M. P. Weinstein, LMS Engineers, pers. comm., 5 October 1983).

Duration of stages

The transitions from stage C to D and D to E were each observed in the laboratory to occur with 24–48 h. The transition from stage E to stage F occurred in 5–10 days, while that from stage F to the juvenile stage is gradual, occurring in the 3 to 9 days after the left eye reached its final position. We infer that stages B–D are of short duration, lasting a few days, while stages E-F last from 1 to 2·5 weeks.

The relative duration of the stages partially explains why stages E and F dominated the catch as each recruitment peak progressed, ana as the season of recruitment progressed. The short duration of stages C and D make their contribution to the catch more important than standing stocks alone would indicate.

Hydrographic measurements

Surface temperatures were consistently between 8·5 and 10·0 °C from January through March but after April were higher and more variable than in the first half of the study [Figure 2(a)]. Bottom temperatures were more similar at the start and end of sampling and were less variable in the second half of the sampling than were surface temperatures [Figure 2(b)]; they showed a pattern similar to surface temperatures but were usually 1–2 °C less. Generally, initial surface temperatures reflect those of the riverine system, with the final bottom temperatures being those of ocean temperatures. Surface salinities were variable from January through April, but were uniformly high in May–July [Figure 2(c)]. Bottom salinities were almost always high [Figure 2(d)] with a gradual increase through the sampling season.

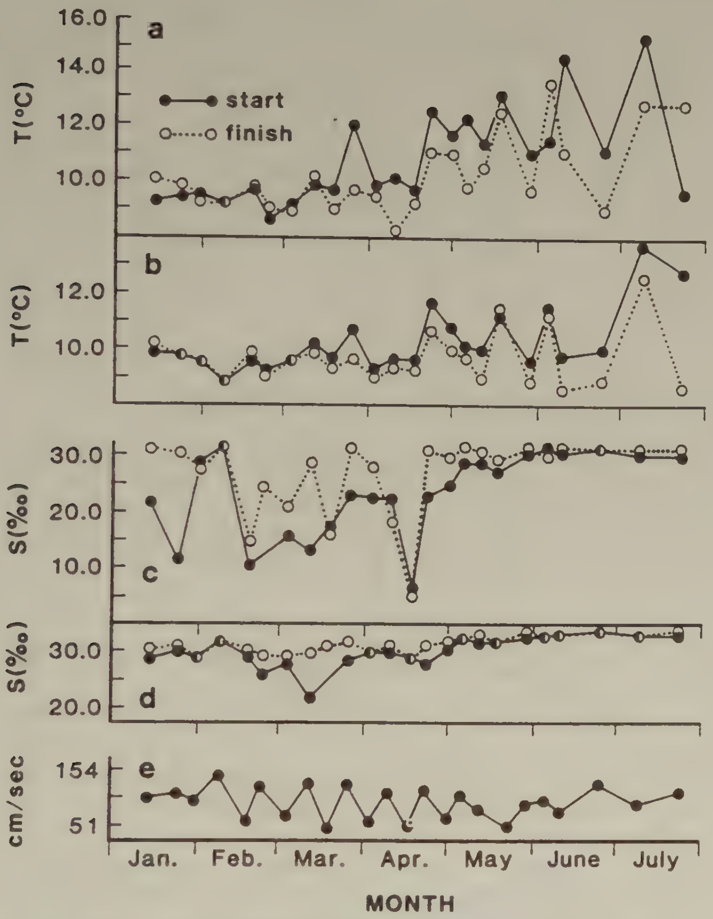

Figure 2. Physical features of Yaquina Bay during the sampling period. For temperature and salinity measurements, the sampling location was at the moored net sampling site; initial values (●) were taken at the start of the flood tides when the moored plankton nets were set, and final values (○), near the end of flood tide when the nets were retrieved. a, Surface temperature (taken with a bucket thermometer). b, Bottom temperature (from Niskin bottle samples). c, Surface salinity. d, Bottom salinity. e, Maximum current speed (cm s^{-1}) taken from tidal current charts (National Ocean Survey, 1981*b*).

Maximum flood tide current speeds (National Ocean Survey, 1981*b*) indicate that our sampling coincided with alternating spring and neap tides from February through April, but was offset from this cycle in May–July [Figure 2(e)]. River discharge was variable with high flow following rainfall on three dates [Figure 3(a)]. The high discharge values show close temporal correlations with low surface salinity values at the start of sampling [Figure 2(c)]. After April, discharge declined to low ($< 4{\cdot}0$ m^3 s^{-1}) summer levels after the end of the winter rains.

The strength of onshore and offshore Ekman transport is estimated by the ‘coastal upwelling index’ [Bakun, 1975; Figure 3(b)]. The transition between winter onshore transport and summer offshore transport (upwelling) occurred in late April, although

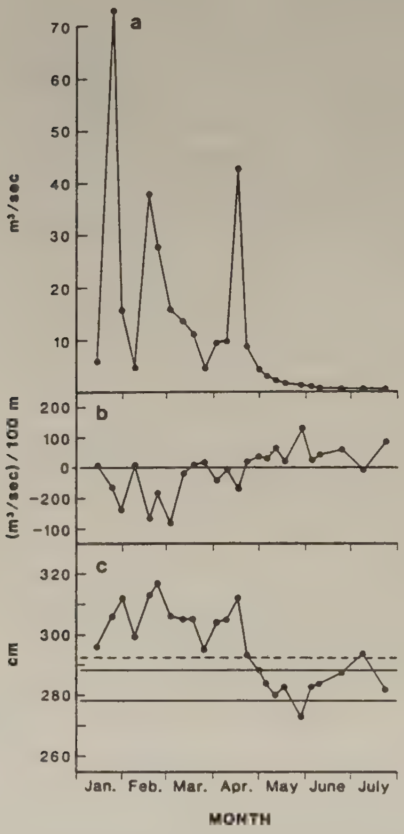

Figure 3. Riverine and ocean conditions during the sampling period. a, Yaquina River freshwater discharge on the day of sampling. b, Bakun upwelling index for 45°N, 125°W. c, Mean sea level at Yaquina Bay. The dashed line in (c) indicates the annual mean sea level (Pittock *et al.*, 1982) and the lower two solid lines represent the range of sea levels associated with zero alongshore current speed (Marthaler, 1977). Values of upwelling index and sea level are means for the seven days preceding the day of sampling.

weeks of reduced zonal transport were found in all months [Figure 3(b)]. Coastal sea level is correlated with current speed and direction over the Oregon shelf (Marthaler, 1977; Kruse & Huyer, 1983). Sea level measurements in 1982 indicate a transition from the winter regime of northward, onshore transport to the summer regime of southward, offshore transport during late April [Figure 3(c)]. A general correlation among river discharge, upwelling index, and sea level is apparent in Figure 3. Moreover, a correlation matrix of the physical factors considered between 23 February and 24 July (Table 1) shows a high degree of intercorrelation of variables, with relatively few being nonsignificant.

Size, stage, and seasonality of larval recruitment

Recruitment of *P. vetulus* to the estuary occurred during transformation; the mean length of pelagic larvae in stages A–F was 19·1 mm SL, and no trend in changing mean length was found over the season of recruitment. Catches of pelagic larvae from surface and midwater

Table 1. Pearson correlation matrix of physical factors considered in the study of recruitment of larval *Parophrys vetulus* to Yaquina Bay, Oregon[a]

	FW	SL	UPW	UPW4	BS	BT	SS	ST	DS
DT	0·50[b]	0·65[b]	−0·49[b]	−0·45[b]	−0·74[b]	−0·48[b]	−0·60[b]	−0·86[b]	0·54[b]
DS	0·77[b]	0·75[b]	−0·35	−0·60[b]	−0·71[b]	−0·37	−0·99[b]	−0·54[b]	—
ST	−0·51[b]	−0·63[b]	0·46[b]	0·50[b]	0·54[b]	0·78[b]	0·60[b]	—	—
SS	−0·78[b]	−0·81[b]	0·41[b]	0·64[b]	0·74[b]	0·41[b]	—	—	—
BT	−0·36	−0·39[b]	0·35	0·32	0·27	—	—	—	—
BS	−0·41[b]	−0·71[b]	0·30	0·86[b]	—	—	—	—	—
UPW	−0·39[b]	−0·72[b]	0·30	—	—	—	—	—	—
UPW4	−0·36	−0·53[b]	—	—	—	—	—	—	—
SL	0·66[b]	—	—	—	—	—	—	—	—

[a] FW, freshwater input to Yaquina Bay; SL, sea level at Newport; UPW, Bakun upwelling index at 45°N 125°W (FW, SL and UPW are all averaged for the 7 days prior to sampling); UPW4, mean upwelling for the previous week; BS, bottom salinity at beginning of sampling; BT, bottom temperature at beginning of sampling; SS, surface salinity; ST, surface temperature; DS and DT, values of the difference between ocean and bay salinity and temperature, respectively, calculated by the difference between the final bottom salinity and temperature and the initial surface values.

[b] Significant correlation ($p < 0·05$).

collections indicate that larvae enter the bay pelagically as the left eye migrates across the dorsal surface of the head, but before the juvenile pigment develops, as found for *Kareius bicoloratus* (Tsuruta, 1978).

An ontogenetic change in depth distribution of pelagic fish was observed [Figure 4(a–c]. Stages A and B comprised a larger proportion of the catch at the surface than at midwater or the bottom, stages C and D were abundant at all depths, and stages E and F were most abundant in the midwater and bottom nets. Thus, later stage larvae may not swim as high in the water column as earlier stage larvae. As shown by the beam trawl collections, however, stages B–F occurred within 0·3 m of the bottom.

Three peaks of larval recruitment were observed in 1982 (Figure 4). The first, 4–25 March, was largest with stages C and D dominating the catch (Figure 4). Initially within this peak, surface densities were greatest; catches in midwater and bottom nets peaked progressively later (Figure 5). After 4 March, however, larval densities were almost always greatest in the bottom net, and larval densities in midwater were generally greater than those at the surface. The second peak occurred from 16 to 22 April. During this brief peak, surface densities were higher in the first week but lower than midwater in the second week. This peak was dominated by stage D at the surface and stages E and F at the bottom. The third peak, from 5 May to 9 June, was more extended than the first two, and larvae were never abundant at the surface. These data suggest that entry into the estuary occurs at all depths, but with a trend for a greater proportion of the larvae to occur deeper in the water column during the course of each peak in larval recruitment. Also fewer larvae are captured at the surface at the beginning of each recruitment peak as the season progresses (Figure 5). Larvae at later stages of eye migration (E and F) composed a greater proportion of the catch as each peak progressed.

Benthic larval densities

The temporal trend in abundance of the larval English sole caught in the beam trawl generally matches that from the moored nets. The three peaks of abundance (during

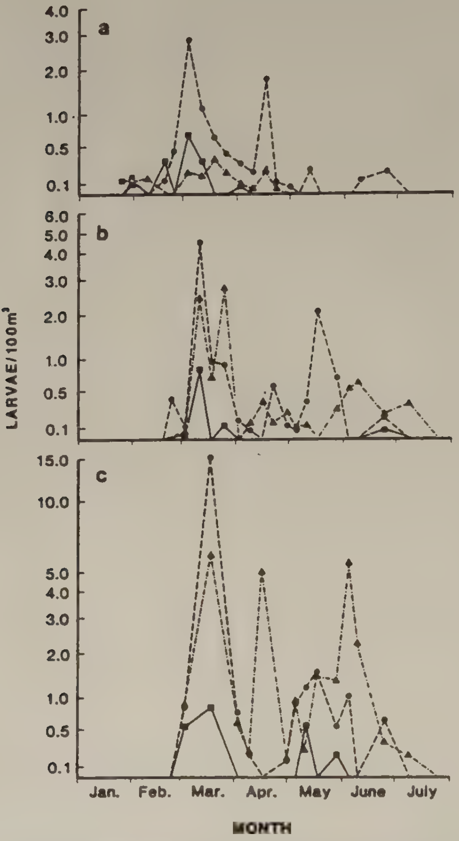

Figure 4. Seasonality of recruitment of different larval stages in surface (a), midwater (b), and bottom (c) moored ichthyoplankton nets. Density estimates shown are the mean of the two replicate samples at each depth. Densities of larval stages: A and B (■), C and D (●), E and F (▲).

March, April, and May) were found in the beam trawl catches, and are reflected in the abundance of stage D–F larvae (Figure 6). Larvae were present in trawl samples at all stages except A. Early stage larvae were rare compared to their relative abundance in the plankton. This suggests that early larvae are either not available to the sampling gear, are flushed from the bay, that the transformation process in early stages is rapid, or that the earliest stages are more vulnerable to predation. Our observations of stage durations support the third hypothesis.

The abundance of completely transformed juveniles followed the temporal pattern of stages B–F in beam trawl samples until late March (Figure 6). After 18 March, the densities of juveniles increased in proportion to those of younger stages. High densities ($> 1\ m^{-2}$) of juveniles were found from 7 April through 9 June, indicating that the strongest cumulative recruitment of young-of-the-year English sole to the estuary occurred prior to this time and was strongest in March–April. Declining abundances in June and July indicated that emigration from these stations and mortality exceeded recruitment, despite continued catches in the moored net samples in June (Figures 4 and 5).

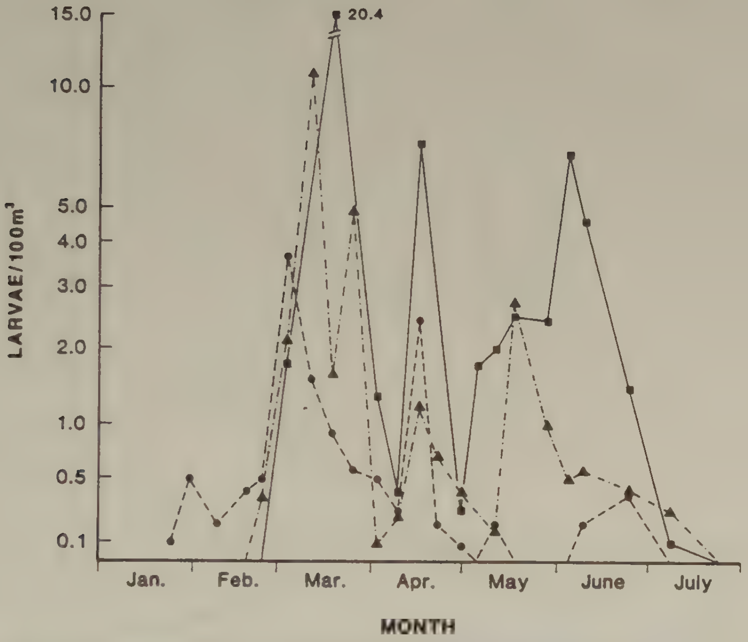

Figure 5. Seasonal densities (larvae per 100 m^3, all stages combined) or larval *Parophrys vetulus* during the 1982 migratory season, as a function of depth of capture. Each value represents the mean of two replicate samples. ●, Surface nets; ▲, midwater nets; ■, bottom nets.

Fortnightly oscillations in the catches of juveniles were superimposed on the seasonal pattern of February–May (Figure 6). High abundances generally occurred on spring tides followed by lower abundances on the neap tides the following week. The oscillation was not apparent after recruitment decreased in June. To test for the relationship of abundance with the neap–spring tidal cycle, the moving average (weighted by one adjacent point earlier and one adjacent point later) for each point of juvenile abundance, from 23 February to the end of the season, was determined. Then, the deviation of these values from observed values was calculated and divided by the moving average for scale. Regressing this value on maximum values of current speed (National Ocean Survey, 1981*b*) during collections shows a significant relationship of scaled abundance with current speed (Figure 7), suggesting that densities are low at the stations during neap tides (when current speed is low). High current speed may result in greater bottom scour in the mid-channel areas; during these times juveniles may seek more protected shallows such as our sampling area. The same relationship, only weaker, held for benthic larvae in stages B–F.

Diel recruitment patterns

Diel sampling on different tides demonstrated that larval *P. vetulus* were only abundant during night flood tides on 17–18 March and 9–10 April (Table 2), supporting the choice of sampling times. No *Parophrys* larvae were taken in daylight ebb and flood tide Tucker trawl samples on 4 May, although they were found in night flood tide moored net collections on 5 May. This trend for highest catches during night flood tides thus occurred

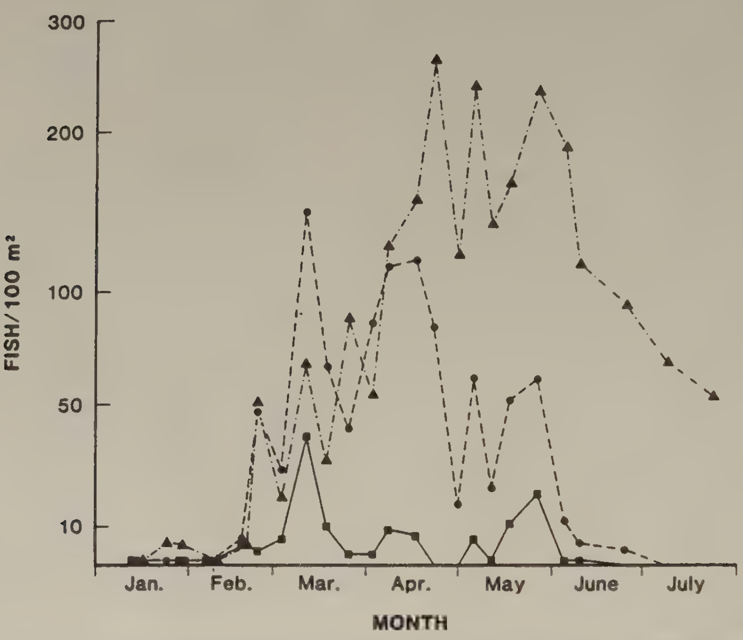

Figure 6. Densities of benthic larval and juvenile *Parophrys vetulus* (numbers per 100 m^2) taken during beam trawl sampling in 1982. ■, Densities of larval stages B–D combined; ●, larval stages E and F; ▲, juvenile fish.

throughout the early part of the season of recruitment. This pattern was not observed during the night ebb and flood tide collections later in the season, when night ebb tide catches were high (Table 3). Very high densities of *Parophrys* larvae were found in Tucker trawl samples from the slack high tide on 20–21 May, relative to densities in Tucker trawl and moored net samples from the ebb tide on 20–22 May and slack low and flood tides on 27–28 May. In addition, densities from bottom moored net samples during the ebb tide on 20–21 May were greater than the densities from bottom moored net and Tucker trawl samples during the slack low and flood tides on 27–28 May. While no simple pattern is seen in these data, it is clear that the pattern of high abundance only during night flood tides was not found in late May. The high abundance from the slack high tide on 20–21 May was found during a week of spring tides, while the lower abundance from the flood tide a week later was found during a neap tide. The occurrence of high abundance during a spring tide is similar to our results from beam trawl catches. Two seasonal factors may be pertinent to the change in pattern of diel abundance near the end of recruitment. Upwelling began in late April (Figure 3), which may have affected the behaviour of *Parophrys* larvae. Emigration of early juveniles from Yaquina Bay began in late May and June (Figure 6; Krygier & Pearcy, 1986), which could have altered the pattern and abundance over the tidal cycle, particularly near the bottom, even though immigration of stages D–F continued during the study (Figure 4).

The relationship of environmental factors to estuarine recruitment of Parophrys vetulus

Parophrys vetulus larvae and juveniles accumulated in Yaquina Bay during 1982 with recruitment extending over a prolonged season, from February to June (Figures 5 and 6).

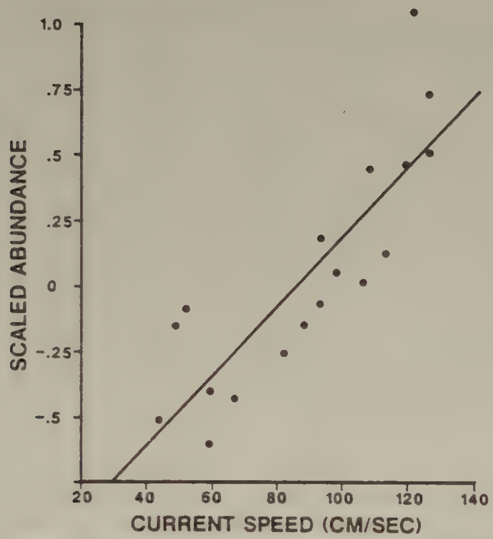

Figure 7. Densities of juvenile *Parophrys vetulus* collected in the beam trawl as a function of current speed. Maximum current speeds were taken from National Ocean Survey (1981*b*). Data points represent sampling times between 23 February and 9 July. Observed abundances were changed to moving averages weighted by one point earlier and later; this value was then subtracted from the observed value and divided by the moving average for scale. Thus positive scaled abundances are greater than expected, negative abundances less than expected. The line is represented by the linear fit scaled abundance $= 0{\cdot}0135$ (current speed) $- 1{\cdot}14$. $N = 18$, $r^2 = 0{\cdot}71$.

During this season, most of the fish entered in pulses. Planktonic larvae entered at all depths, but the proportion of larvae entering at the surface was usually greatest earlier in the peak than later. Benthic juvenile density increased from February through April but not as rapidly in March as would be expected from the large pulse of pelagic and benthic larvae (Figures 5 and 6). The major increase of benthic juveniles occurred in April, during the second peak of recruitment which was the least pronounced of the three for pelagic larvae. Although the third peak of pelagic larval recruitment was prolonged, from mid-May through mid-June, densities of benthic juveniles declined during that time.

Accumulation of larval *P. vetulus* in nearshore areas by onshore Ekman transport appeared to be important during the period of larval recruitment from mid-February to June (Figures 5 and 6). A period of onshore transport [Figure 2(b)] preceded the first peak of larval recruitment by a week (Figure 4). The strongest peak of onshore transport (in early March) coincided with the greatest recruitment of pelagic larvae at the surface, and preceded the largest peak of benthic larval recruitment by a week. The final two periods of onshore transport (in April) coincided with the major increase in abundance of benthic larvae and juveniles. The relationship was not observed during the final pulse of recruitment in May and June, when surface water transport was offshore; these recruits were typically later stages which may have come from nearshore nursery areas (Figure 4). The sea level record [Figure 3(c)] matched the recruitment of *Parophrys* in the same way as the upwelling index record, but the relationship of peaks in transport to pulses of recruitment was not as clear.

A direct relationship of river discharge [Figure 3(a)] to recruitment was not found. The largest peak in discharge preceded recruitment of *Parophrys* in January. The next peak in

Table 2. Density of *Parophrys vetulus* larvae (individuals per 100 m^3) taken at each depth on each tide during diel sampling[a]

	Moored nets			Tucker trawl		
	Depth			Depth		
Date 1982/Tide	S	M	B	S	M	B
17–18 March						
Day flood	0	0	0	—	—	—
Day ebb	0·91	—	—	—	—	—
Night flood	0·90	1·60	19·75	—	—	—
Night ebb	0	0	0·64	—	—	—
9–10 April						
Day slack low	—	—	—	0	0	0
Day flood	0·04	0	0	0	0	0
Day slack high	—	—	—	0	0	0
Day ebb	0	0	0	0	0	0
Night slack low	—	—	—	0	0	0·92
Night flood	0·26	0·20	0·43	0	1·28	2·06
Night slack high	—	—	—	0	0	0
Night ebb	0·07	0	0·20	0	0	0·12
4–5 May						
Day flood	0	0	0	0	0	0
Day ebb	—	—	—	0	0	0
Night flood	0	0·17	1·73	—	—	—

[a] Each value is the mean of two samples. S, Surface; M, midwater; B, bottom nets; ——, no sample.

Table 3. Density of *Parophrys vetulus* larvae (individuals per 100 m^3) taken at each depth on each tide during night sampling from 20 to 28 May 1982[a]

	Moored nets			Tucker trawl		
	Depth			Depth		
Date 1982/Tide	S	M	B	S	M	B
20–21 May						
Night slack high	—	—	—	8·17	5·93	8·96
Night ebb	0·31	0·27	4·87	—	—	—
22 May						
Night ebb	0·34	0·65	—	0·43	0·64	0·26
27–28 May						
Night slack low	—	—	—	0·45	0·12	0
Night flood	0	0·96	2·40	0·12	0·22	0·42

[a] Each value is the mean of two samples. S, Surface; M, midwater; B, bottom; ——, no sample.

Table 4. Pearson correlation matrix of larval densities with physical factors^{a}

	FW	SL	UPW	UPW4	BS	BT	SS	ST	DS	DT
ADS	0·68^{b}	0·65^{b}	−0·68^{b}	−0·60^{b}	−0·62^{b}	−0·47^{b}	−0·77^{b}	−0·63^{b}	0·76^{b}	0·56^{b}
ADM	0·04	0·19	−0·18	−0·46^{b}	−0·61^{b}	−0·08	−0·34	−0·22	0·34	0·37
ADB	−0·01	0·17	0·02	−0·25	−0·41^{b}	−0·23	−0·28	−0·36	0·30	0·40
AD	0·16	0·27^{b}	−0·19	−0·37^{b}	−0·48^{b}	−0·22^{b}	−0·38^{b}	−0·36^{b}	0·39^{b}	0·40^{b}
EFS	0·49^{b}	0·56^{b}	−0·29	−0·38^{b}	−0·45^{b}	−0·37	−0·65^{b}	−0·38^{b}	0·67^{b}	0·29
EFM	0·07	0·18	−0·07	−0·26	−0·51^{b}	−0·17	−0·30	−0·18	0·32	0·15
EFB	0·17	0·08	0·12	0·05	−0·20	−0·12	−0·23	−0·05	0·25	0·11
EF	0·11	0·10	0·02	−0·06	−0·22^{b}	−0·11	−0·20	−0·08	0·21	0·10

^{a}ADS, ADM, ADB, AD, log-transformed densities of stages A–D at surface, midwater, bottom, and all nets combined, respectively. EFS, EFM, EFB, EF, log-transformed densities of stages E and F in surface, midwater, bottom, and all nets combined, respectively. For description of physical factors, see Table 3.
^{b}Significant correlation ($p < 0.05$).

discharge, in late February, coincided with the onset of estuarine recruitment. Discharge was moderate during the peak of larval recruitment in March. The final discharge peak, in mid-April, coincided with the second pulse of recruitment, when juvenile *Parophrys* accumulated in the bay. Discharge declined to low spring and summer levels in May and June, during the final pulse of recruitment.

Clear differences exist in the times and depths at which different stages recruited to the estuary (Figure 4), so it is not unexpected that relationships between physical factors and recruitment will vary among stages and in the different nets. To examine the differences, densities of pelagic larvae were combined by stages A–D and by stages E and F to correlate with the physical variables (from Table 1). Correlations of the physical factors with early stage (A–D) densities are stronger than for the late stage (E and F) densities (Table 4). This may be due to the duration of the stages, with the more ephemeral early stages showing a closer relationship with conditions at the time of their capture. Secondly, within both groups, correlations are typically significant in the surface net samples, but poor in the midwater and bottom nets.

As described above, onshore transport brings transforming larvae to nearshore areas and is responsible for the major pulses of early stage larval recruitment (Figures 4–6). This is reflected in the negative correlation between mean upwelling for the week of sampling (i.e. offshore transport) and early stage larval densities in surface samples (Table 4). The lack of significant correlation between upwelling and later stage larval recruitment suggests that other factors influence their recruitment. Larvae recruited to nearshore nursery areas (Laroche & Holton, 1979; Krygier & Pearcy, 1986) begin the transformation process, and may use a different mechanism for locating and recruiting to the estuary. This is supported by the stronger correlation of upwelling lagged by a week to the various larval densities (Table 4).

For this group, which we call the nearshore recruitment pool, the strongest correlation is with bottom salinity at the start of sampling (BS, Table 4), which shows a strong negative correlation with densities of virtually all groups. While this might infer that freshwater input to the estuary is the causative factor, the correlation of input with recruitment is weak, with the exception of surface catches (Table 4). As expected, surface salinity shows a similar trend, with greater surface recruitment during times of low salinity. Bottom salinity is weakly correlated with freshwater input as compared to surface salinity, but strongly correlated with sea level and with lagged upwelling (Table 1). This suggests that lowered bottom salinity as the ebb tide begins may play a role in the movement of animals from the nearshore recruitment pool.

Discussion

Several studies have documented a relationship between physical factors and recruitment of fishes, generally by correlating onshore transport with year class strength (Nelson *et al.*, 1977; Bailey, 1981). The implication is that larval drift in the wrong direction prevents movement to the appropriate nursery areas (whether coastal or estuarine) and that the resultant cohort will show poor survival; this concept dates back to Hjort (1914) and has been placed in the context of current patterns of the west coast of North America by Parrish *et al.* (1981). This type of relationship is unclear for *P. vetulus*. Ketchen (1956) showed an inverse correlation between temperature during development and subsequent year-class strength; he inferred that lower temperatures delayed development, resulting in extended pelagic existence and more complete drift to nursery areas before metamorphosis. Higher temperatures presumably resulted in rapid metamorphosis prior to availability of habitat for settlement, which may cause high mortalities (Marliave, 1977).

Subsequent studies dealing with a larger body of fishery data have not made the situation clearer for *P. vetulus*. Hayman and Tyler (1980) suggested that upwelling during the fall delayed spawning and that this was in some way linked to stronger cohorts. Kruse (1984), with a more sophisticated model, did not link recruitment success to either storm effects or starvation (as reflected in primary production), but to indices of larval transport. Larval *P. vetulus*, however, are consistently found in the coastal assemblage of fish larvae (within 28 km of shore) under various environmental regimes (Richardson & Pearcy, 1977; Laroche & Richardson, 1979; Richardson *et al.*, 1980; Mundy, 1984). Therefore, this species may control its onshore–offshore distribution through some form of modulated transport akin to the mechanism proposed by Peterson *et al.* (1979) and Rothlisberg and Miller (1983). The general picture of planktonic population maintenance over continental shelves, however, is probably more complex; Sundby (1984) showed that eddies produced by flow–topography interactions may retain fish eggs on the continental shelf of Norway. On the shelf off the west coast of North America, a similar phenomenon may occur because most cross-shelf transport occurs in localized jets (Mooers & Robinson, 1984). Within a given year, however, our data suggest that onshore transport is important in the pulses of recruitment to Yaquina Bay (Figures 3 and 5). Transforming larvae are abundant in neuston collections within 30 km of shore, where densities reached 75 per 10^3 m^2 (J. Shenker, Bodega Bay Marine Laboratory, Sonoma, CA 94923, pers. comm., 9 May 1985). Larvae occurring in the neuston may be subject to a greater probability of onshore transport by wind-driven advection than larvae occurring throughout the water column (Parrish *et al.*, 1981); further, Shanks (1983, 1985) has shown that neustonic species may accumulate and be transported onshore in surface slicks associated with internal waves.

A comparison of the life history of *P. vetulus* with many of the species subject to offshore transport effects (hake, menhaden) shows that one important difference is in timing of spawning. English sole are unlike other marine species in that the spawning season is prolonged and variable from year to year, apparently subject to thermal conditions in the benthic habitat; Kruse and Tyler (1983) found that spawning occurred between September and April, with a peak lasting 1–3 months within this interval. As spawning is triggered by warming of shelf waters, it coincides with periods of onshore transport which may maintain eggs and early larvae in the nearshore zone. Further, feeding ecology may play a role in larval survival. Gadomski and Boehlert (1984) demonstrated that larval English sole depend upon appendicularians as prey organisms. Appendicularians show peaks of abundance which are also associated with periods of onshore transport of low salinity water (Peterson & Miller, 1976) and are often highly aggregated (Alldredge, 1982). Thus an understanding of the year-class strength of this species may require further analysis of the match–mismatch hypothesis of Cushing (1975). Despite several studies considering environmental factors and year-class strength (Ketchen, 1956; Hayman & Tyler, 1980; Kruse, 1984), the stage at which year-class strength is determined for English sole has not been clearly defined. However, in the most comprehensive study to date comparing mortalities of pelagic and estuarine demersal stages of a flatfish, van der Veer (1986) noted that overall year-class strength in plaice was determined prior to settlement but that density-dependent mortality in the estuary served a modulating effect, significantly decreasing the variability in year-class strength.

Estuarine dependence for species with eggs and larvae spawned offshore is rare on the Pacific coast of North America. By comparison, Miller *et al.* (1984) showed that five fishes representing 85% of the commercial fisheries catch in North Carolina have this life history pattern. It is significant in this regard that the one marine species with an estuarine-dependent juvenile stage on the Pacific coast is a flatfish. We have suggested a dual pattern of estuarine recruitment, with the earliest pulses being transforming pelagic larvae and then continued recruitment of a nearshore recruitment pool of older larvae. This interpretation agrees with data in Krygier and Pearcy (1986), who observed a dcrease in density of juveniles in nearshore nursery areas concurrent with density increases in Yaquina Bay. Near metamorphosis, flatfishes undergo significant morphological and behavioural changes (Finger, 1976; Tsuruta, 1978; Kawamura & Ishida, 1985) which allow transition from pelagic to benthic existence. Maintenance of a nearshore pool of recruits would be difficult for fishes not associated with the bottom, such as the estuarine recruiting sciaenids and clupeids of the Atlantic and Gulf coasts. Flatfish, however, can remain on the bottom, like recruiting *Anguilla* (Creutzberg, 1961; McCleave & Kleckner, 1982) or shrimps (Hughes, 1969; Staples, 1980), as demonstrated by the abundance of transforming pelagic larvae in our beam trawl samples (Figure 6). This group of larvae can affect their horizontal distribution by moving into the water column, as transforming flatfish may show an ambivalence between pelagic and benthic behaviour (Fluchter, 1965).

While initial recruitment is related to onshore transport, subsequent entry to the estuary by the nearshore pool of recruits is apparently related to estuarine factors, as recruitment occurs primarily on night flood tides (Table 2). Larvae in stages E and F are most indicative of this pattern, and the dominant factor correlated with larval abundance is bottom salinity at the start of sampling. While this is not strongly correlated with freshwater input, as one would suspect, it may instead be a function of turbulence within the estuary. Locating the estuary may thus be a function of low salinity water flowing out near the bottom, which could result in activity patterns such as pelagic swimming (Creutzberg *et al.*, 1978). Reference to either the bottom or endogenous, rhythmic activity may then signal the end of flood tide and of pelagic activity (Boehlert & Mundy, in press). Such behaviour would increase the probability of transport into the estuary (Tsuruta 1978; Rijnsdorp *et al.*, 1985). This movement is a form of tidal stream transport and can save up to 90% of the energy necessary for migration (Weihs, 1978). That it is a directed movement is obvious by comparing densities of transforming larval *Parophrys* in the estuary with passively recruited larvae of other species (Pearcy & Myers, 1974; Boehlert & Mundy, in press). When samples from the present study were later sorted for smaller larvae, only five *Parophrys* larvae smaller than 10 mm SL were found (Mundy & Boehlert, unpubl. data); these early larvae apparently enter the estuary by passive movement.

While the sampling did not expressly study emigration from the estuary, the data on juvenile abundance (Figure 6) suggest that emigration began in late May while immigration of larvae was still occurring (Figures 4 and 5). Pelagic emigrants in late May (Table 3) did not differ in development stage from immigrants seen at the same time period. Early in the season, virtually all pelagic activity by larvae takes place on night flood tides (Table 2), whereas late May samples show activity by larvae on night slack high and the following ebb tide (Table 3). This contrasts with the observations of Rijnsdorp *et al.* (1985) and van der Veer (1986), who noted that early-stage larvae recruited on flood tides but were often flushed from the estuary on the following ebb tide. Development of behaviour patterns with age is probably an important factor in estuarine retention (Fortier & Leggett, 1982; Epifanio *et al.*, 1984). While the study involved too few samples to determine the relationship of temperature, salinity, or other factors with the difference between the early and late season samples, the pattern of juvenile abundance (Figure 6) and its relationship with the spring–neap cycle (Figure 7) may help explain the difference. It is possible, for example, that the increased densities during periods of high current speed may be from movement of fish from farther up the estuary to the region sampled near the mouth (Figure 1). Rijnsdorp *et al.* (1985) found higher larval densities correlated with increased suspended material and suggested that larvae are ' swirled up from the bottom ' like the suspended matter, and perhaps flushed from the estuary. While this is possible, it was not observed in this study [Tables 2 and 3; Figure 2(e)].

The recruitment dynamics of English sole to Yaquina Bay show a more complex pattern than those reported for many Atlantic species using larger estuarine nursery areas (Creutzberg, 1961; Weinstein *et al.*, 1980; Miller *et al.*, 1984). Accumulation of *P. vetulus* larvae in nearshore areas, and the initial pelagic recruitment to estuaries, is related to onshore transport in a relatively simple way. Recruitment to the estuary, however, also appears to occur from some of the later stage larvae and juveniles which have settled in open coast areas (Rogers, 1985; Krygier & Pearcy, 1986). A more complicated relationship exists between recruitment and reduced bottom salinities, perhaps in connection with moderately high river discharge. The reduced salinity may serve not only to influence behaviour that would enhance tidal stream transport of recruits entering the estuary directly (Creutzberg *et al.*, 1978), but may also influence fish recruiting to the estuary from coastal areas. This more complex recruitment pattern may enhance the ability of *P. vetulus* to use the relatively small, isolated west coast estuaries as juvenile nursery areas.

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Reproductive mode and energy costs of reproduction in the genus *Sebastes*

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The genus *Sebastes* has historically been considered to be ovoviviparous, with all energy for embryonic development coming from the yolk present at fertilization. Recent studies have shown that embryos of two species receive nutrition in addition to that supplied in the yolk. Embryonic catabolism (estimated from *in vitro* oxygen consumption) required a significant portion of the yolk energy; combined with energy content of the larva at birth, total energy was much greater than the initial egg energy. One can access the accuracy of *in vitro* embryonic oxygen consumption by determining the excess respiration by pregnant females above that of males and immature females. In *Sebastes schlegeli*, this excess oxygen consumption is significant. The additional oxygen consumed by gestating females is greater than that predicted for oxygen consumption of the embryos early in gestation but less later in gestation, suggesting that *in vitro* estimates are approximately 80% high. We discuss the implications of these estimates to earlier calculations of viviparity. Energy taken up through ingestion and absorption of ovarian fluid in the hindgut, however, still confirms viviparity.

Introduction

Live-bearing fishes are characterized by a wide range of energetic relationships between maternal and embryonic systems. The genus *Sebastes* has historically been considered to be ovoviviparous, and that no additional nutrition is provided to the embryo during gestation (Scrimshaw 1945; Amoroso 1960). The reasons for this description have been based upon inference, however, since initial egg size is small, larvae are small at birth, and fecundity is very high (Phillips 1964; Moser et al. 1977; Boehlert et al. 1982). Recently, however, energetic studies have demonstrated that embryos of two rockfish species receive some form of nutrition during later stages of gestation and are thus viviparous (Boehlert and Yoklavich 1984; Boehlert et al. 1986). The source of nutrition was postulated to be a nitrogenous substance derived from resorption of unfertilized ova through ingestion of ovarian fluid and subsequent uptake in the hindgut.

The work demonstrating viviparity compared indirect with direct calorimetry of embryos during development. The indirect calorimetry used *in vitro* oxygen consumption to determine catabolic needs in development. Oxygen consumption *in vitro* increases with increasing developmental stage either linearly (*S. melanops*, Boehlert and Yoklavich 1984) or exponentially (*S. caurinus*, Dygert 1986; *S. schlegeli*, Boehlert et al. 1986). An important assumption of all previous work is that *in vitro* oxygen consumption is closely related to that *in vivo*. Many studies have estimated embryonic oxygen consumption of live-bearers *in vitro* (Moser 1967; Webb and Brett 1972; Berglund et al. 1986), but few have considered oxygen consumption rates *in vivo*. Boehlert et al. (1986) questioned the accuracy of *in vitro* oxygen consumption rates and suggested that they may be higher than *in vivo* rates, thus inflating estimates of catabolic energy use. In this paper we discuss the manner in which viviparity was demonstrated in *S. melanops* and *S. schlegeli* and then, by considering the relative increase in oxygen consumption by gestating female *S. schlegeli* as compared with spent or immature females or males (Webb and Brett 1972), provide insights to the accuracy of the *in vitro* measurements.

Materials and Methods

Methodology used in the embryonic energetics studies has been described in Boehlert and Yoklavich (1984) for *S. melanops* and Boehlert et al. (1986) for *S. schlegeli* and will be only briefly described here. Developmental stages of embryos were classified according to a modification of Oppenheimer (1937) and Yamada (1963) (Kusakari unpublished). Gestation time and duration of different stages of development were determined from samples of embryos taken from females held in the laboratory. Fish were catheterized at various intervals and an analytical relationship between the stage of development and the duration of each stage was developed. From this relationship stage of development was converted to time since fertilization.

Oxygen consumption was determined for embryos at several stages of development in a Gilson differential respirometer at 10°C using standard techniques (Umbreit et al. 1972). At the end of each experiment, the embryos were counted and used for dry weight and carbon and nitrogen determinations; some embryos were preserved for determination of developmental stage. Ash-free dry weight (AFDW) was determined from groups of 35-100 embryos. Caloric content was determined from percent carbon using the nitrogen-corrected equation of Salonen et al. (1976).

For experiments on respiration rates of adult *S. schlegeli*, fish from captive populations were used. Two days before beginning experiments, fish were weighed, measured, and sex determined after anesthetization in MS-222. Females were catheterized, developing embryos removed and staged, and estimates of time since fertilization (as a function of developmental stage) were calculated following techniques of Boehlert et al. (1986).

Fish were starved at least 2 d before respiration experiments. The respirometer consisted of a cylindrical fish chamber constructed of acrylic tubing 20 cm in diameter with a volume of 13.2 liters. The respirometers were held in a 1.8 x 1.1 x 0.65 m tank which was partially covered with black plastic during experiments. Fish activity and oxygen content of the outflowing water were monitored at 5-10 min intervals. Flow-through methodology was used and oxygen concentrations determined with a polarographic oxygen electrode. Oxygen consumption rates (ml O_2/h) were determined by multiplying the change in oxygen concentration of inflowing and outflowing water by the flow rate. For each animal, a mean value was computed from two replicates. Our estimates may be considered "routine" metabolic rate (Fry 1971). Control experiments were run with empty respirometers and the drop in oxygen content was negligible.

Specimens in our experiments were divided into two groups based upon reproductive status. The first group was composed of males, immature females, and spent females and the second group females with gestating embryos at different stages of development. Respiration rates as a function of weight for the first group were fitted to a curve which could then be used as a predictive model of "normal" or non-gestating respiration rates. The estimates of this curve could then be applied to the second group; the difference between observed and predicted respiration rates was attributed to oxygen consumption by embryos within the female system plus associated costs of live-bearing.

Results and Discussion

Stage duration calculations show that early stages are passed through rapidly and that later stages, which encompass more significant morphological change, take considerably longer. The integrated relationships suggest that fertilization to birth takes 37 d for *S. melanops* (Boehlert and Yoklavich 1984) and 51.5 d for *S. schlegeli*, which has a significantly larger egg (Boehlert et al. 1986). Comparisons of these estimates with data from individual females show agreement but may be somewhat variable under natural conditions. Oxygen consumption, which was determined for both species from embryos at several developmental stages, increased with time since fertilization; the relationship was nearly linear for *S. melanops* (Boehlert and Yoklavich 1984) and was exponential for *S. schlegeli* (Fig. 1). For embryos in later stages of development, many hatched from the delicate chorion and limited swimming activity occurred in the respirometer flasks. This may result in inflated values of oxygen consumption for late stage embryos.

The curves, fitted to the oxygen consumption as a function of time since fertilization, were integrated to estimate the total oxygen consumed during gestation. This value can be converted to calories using an oxycalorific equivalent (Lasker 1962) to determine the total catabolic energy expenditure during gestation. A comparison of these data with the actual energy contained in the embryos (Table 1) suggests that additional energy must be used during gestation. If *Sebastes* was strictly ovoviviparous, the sum of final embryonic

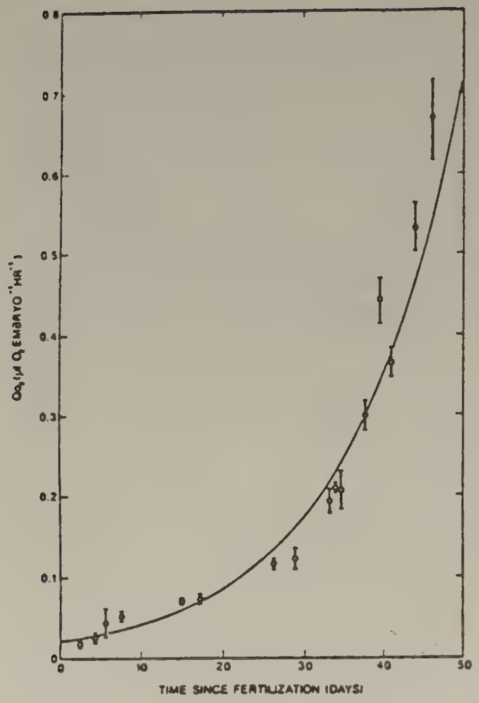

Figure 1. Oxygen consumption in embryonic *Sebastes schlegeli*. Each point (±2 SE) represents the mean of three or four replicates with embryos from the same female (from Boehlert et al. 1986).

Table 1. Changes in the energy content of individual embryos of *Sebastes* from direct estimates of caloric content compared to catabolic energy utilization estimates (from Boehlert and Yoklavich 1984; Boehlert et al. 1986).

	Sebastes schlegeli	*Sebastes melanops*
Initial caloric content	1.59	0.43
Final caloric content	1.48	0.35
Catabolic calories	1.40	0.28

caloric content and catabolic energy utilization during gestation should equal the initial caloric content. The sum is significantly greater for both species, but more so for *S. schlegeli*.

The relative changes in these values during gestation is graphically illustrated for *S. schlegeli* in Figure 2. The catabolic and direct comparisons of energy utilization diverge relatively early in *S. schlegeli*, and the results are clearly indicative of additional nutrition provided to the embryos during gestation. The catabolic energy utilization suggests that the percentages of original yolk energy remaining at birth would be 36% for *S. melanops* and only 12% for *S. schlegeli* (Table 1; Fig. 2).

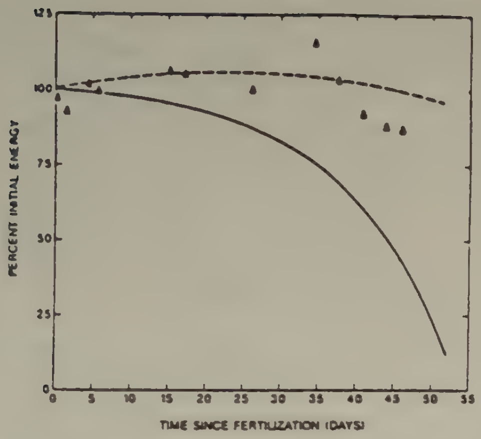

Figure 2. Summary of the energetics of development in embryonic *Sebastes schlegeli*. The y-axis is the percent initial energy, where 100% represents 1.59 calories. The solid line represents expected energy remaining with time based on subtraction of cumulative catabolism. The dashed line and data points represent actual caloric content of embryos at different stages (from Boehlert et al. 1986).

As mentioned earlier, overestimating embryonic respiration could also result in overestimates of catabolic energy utilization. There are two major factors which may be possible sources of error. First, activity by later stage embryos when removed from the maternal system may increase oxygen consumption. As an example, "active" respiration rates for Pacific sardine larvae may be from 1.3 to 3.5 times those of "inactive" rates (Lasker and Theilacker 1962). Second, oxygen tension in the Gilson respirometer is initially at saturated, atmospheric levels (Umbreit et al. 1972) whereas oxygen tension inside the ovary may be low; low ambient oxygen can lower respiration rate in embryos (Carlson and Seifert 1974). It is therefore possible that the rate of development of embryos *in vivo* may be under the control of oxygen availability and that the long gestation times and stage durations may be a result. Although there is no evidence for this in *Sebastes*, Triplett (1960) noted more rapid development *in vitro* for embiotocid embryos.

Respiration measurements on adult *S. schlegeli* were thus used as a check on *in vitro* measurements. Gestating fish were typically much more robust at a given length than were male, immature female, or spent females. The weight increase of gestating females over non-gestating *S. schlegeli* is most marked after about 32 cm SL and the divergence between the two curves increases with increasing length, most likely due to the rapidly increasing fecundity with length. We determined oxygen consumption rates for 23 non-gestating fish, including 19 males, 2 immature females, and 2 spent females for comparison with rates for 17 pregnant females with embryos between stages 1 and 30. Respiration rates typically increased with increasing body weight for non-gestating and gestating fish (Fig. 3). Data from non-gestating fish were fitted to the curve

$$Q = 46.734\ W^{0.7515} \qquad n = 23 \qquad r^2 = 0.524 \quad , \qquad (1)$$

where Q = oxygen consumption rate (ml O_2/h) and W = body weight (kg). At a given body weight, respiration rates were much higher for females with developing embryos. Data from these females were fitted to the curve

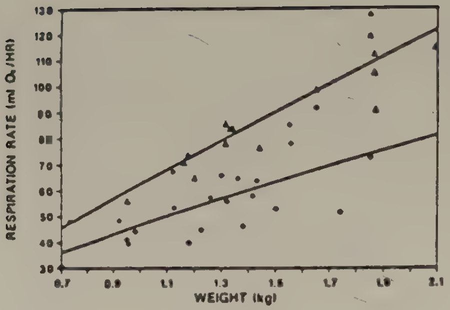

Figure 3. Oxygen consumption rates (ml O_2/h) as a function of fish body weight for Sebastes schlegeli. Triangles represent values from gestating females, and diamonds for males, immature females, and spent females; lines represent fitted curves (from Boehlert et al. in prep.).

$$Q = 62.383\ W^{0.9014} \qquad n = 17, \qquad r^2 = 0.81 \quad . \qquad (2)$$

These two curves (Fig. 3) are significantly different (analysis of covariance, $P < 0.01$). Differences are even more profound when comparisons are made for fish of equal length due to a much greater weight-at-length for pregnant females.

"Excess respiration" may be defined here as the amount of oxygen consumed by a gestating female in excess of that predicted for a non-gestating fish of the same length (Equation 1). This value will be the sum of embryonic respiration requirements and additional live-bearing costs, which include work associated with increased cardiac and branchial pumping and the added costs of ionic and osmotic regulation as more blood passes the gills. Calculation of this value is confounded by the weight of the female fish and the stage of development of the embryos. For this reason we standardized the measured oxygen consumption rates of gestating females (using the weight exponent in Equation 2) to a uniform weight of 1.5 kg. This value corresponds to a fish of 35.6 cm SL, with estimated post-fertilization fecundity of 126,921 embryos (Boehlert et al. 1986) and estimated total embryonic oxygen requirement (fecundity times in vitro embryonic oxygen consumption) which varied with stage of embryonic development from 3.13 to 74.86 ml O_2 h^{-1}. A fish of this length in non-gestating condition would have a corresponding weight of 1.3 kg with a respiration rate of 56.92 ml O_2 h^{-1} (Equation 1). The mean excess respiration of these adjusted data is 33.39 ml O_2 h^{-1} and values show a positive relationship with total embryonic oxygen demands. Subtracting the embryonic respiration rate from the excess respiration, however, results in values which show a negative relationship with the time since fertilization (Fig. 4). This relationship suggests that the added oxygen consumption of gestating females is high early in gestation and decreases, eventually becoming negative with further embryonic development (Fig. 4). The value approaches zero at about 30 d, near the time when the mouth opens and ovarian fluid is apparently consumed (Boehlert et al. 1986). Embryos at this stage are characterized by pigmented eyes, nearly complete lens, and fully formed otoliths, rectum, and urinary bladder (Kusakari unpublished).

If we assume that activity in post-30 d embryos is a major cause of increased in vitro embryonic respiration rates, we can estimate the pattern of respiration without these data. Refitting the curve for

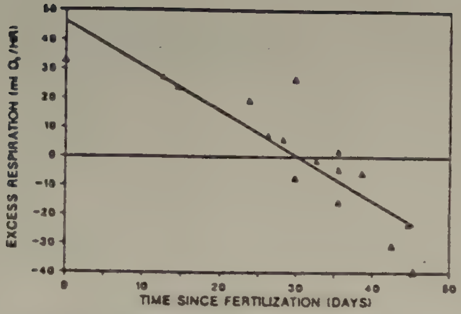

Figure 4. Elevation of respiration rate above that attributed to embryonic respiration in gestating female *Sebastes schlegeli* as a function of time since fertilization. All values are standardized to a weight of 1.5 kg for the gestating female (from Boehlert et al. in prep.).

embryonic oxygen consumption (Fig. 1) with only those values less than 30 d since fertilization allows recalculation of total respiration, which would be 0.70 catabolic calories per embryo. Compared to the estimated *in vitro* catabolic utilization of 1.40 cal (Table 1), the values of *in vivo* embryonic respiration may be inflated by as much as 85%.

Respiration rates may be indirectly estimated by another method as well. Boehlert et al. (1986) suggested that the additional nutrition for embryos comes from resorption of those embryos dying early in gestation. If we assume that this is the only source of energy, then from an energy standpoint the ovaries are a closed system. This would assume that the maternal system only provides exchange of respiratory gases and metabolic waste products. This idea is supported by observed ingestion of yolk proteins by late stage embryos during a time when such materials are not present in the plasma of females (A. Takemura and K. Takano pers. commun.). The energy decrease in the ovary during gestation for the 1.5 kg female *S. schegeli* is about 95.2 kcal. This is based upon the reduction in fecundity (by embryo death) and the decreased energy content per newly hatched larva as compared to a newly fertilized egg (Table 1). Partitioned over the embryos which survive, this amounts to some 0.75 cal each, which is close to the *in vivo* catabolic estimate derived above.

From these results, it would appear that the *in vitro* estimates of catabolic energy utilization by embryos of *S. schlegeli* (Boehlert et al. 1986) are high. If the value is indeed near 0.75 cal, the catabolic curve for *S. schlegeli* (Fig. 2) would show about 53% of the initial energy remaining at birth, still below that estimated by direct calorimetry. Other evidence also supports viviparity. First, uptake of substances by the hindgut occurs in late stage embryos of both species studied (Boehlert and Yoklavich 1984; Boehlert et al. 1986). Further, in individual *S. schlegeli* embryos, ash-free dry weight increases with time since fertilization, and significant decrease in carbon and increase in nitrogen (as a percentage of AFDW) occur during gestation (Fig. 5). The increasing AFDW and increasing percent nitrogen combine to result in a marked increase in nitrogen over the course of development, unlike most oviparous fishes, which show significant decreases in nitrogen over development (Rogers and Westin 1981).

The ovarian oxygen demand from embryonic respiration represents a significant proportion of the gestating female's excess respiration.

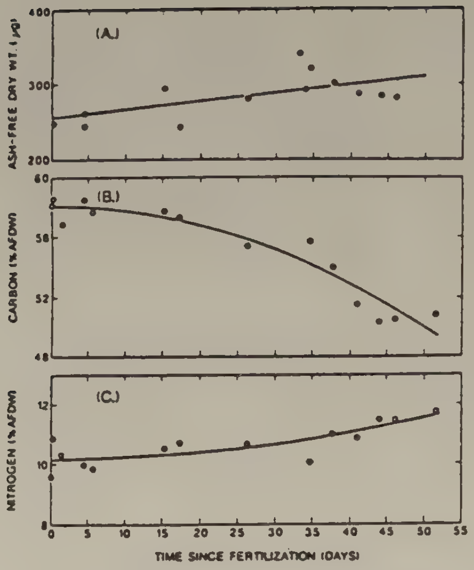

Figure 5. Changes in embryonic ash-free dry weight (AFDW) (A), carbon (B), and nitrogen (C) as a function of time since fertilization (days). Carbon and nitrogen are both expressed as percentages of ash-free dry weight (from Boehlert et al. 1986).

The other part of this excess is apparently associated with costs of live-bearing, including supply of respiratory gases and removal of waste products. That the total "excess" respiration of females during the gestation period remains fairly constant, however, suggests there is some "upper limit" for oxygen consumption. Metabolic scope may be defined as the difference between the maximum active metabolic rate supportable by aerobic metabolism and standard metabolic rate (Fry 1971); this topic has recently been reviewed by Priede (1985). Although the added weight and respiratory demands of developing embryos will contribute to a general decrease in the metabolic scope, other factors must also be considered, including general swimming activity and energy for digestion (specific dynamic action, SDA; Beamish 1974). Vahl and Davenport (1979) demonstrated an increase of 60% in the metabolic rate in Blennius pholis associated with a large ration and attributed this increase to apparent SDA; they suggested that in this fish and other species a single large ration may decrease the scope for activity by some 50% for several hours. Priede (1985) suggested that many fish species must time their feeding activity to keep the metabolic rate within the limits of metabolic scope. Over the extended period of gestation, Sebastes may need to make accommodations for the reduced metabolic scope associated with the increased respiratory load. Sebastes females store significant amounts of fat which are apparently depleted during the gestation period (Guillemot et al. 1985). Interannual variability in environmental factors may result in variability in the level of nutrition provided to embryos in other viviparous fishes (Trexler 1985). The effects of fish size, food availability, and physical factors thus have important implications to reproduction in the genus Sebastes.

Acknowledgments

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Long-term cycles of growth in *Sebastes*: Extracting information from otoliths

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Time series of information about fish populations are useful in understanding their natural fluctuations and responses to variation in physical factors. Most time series on fish, however, concern population size, typically estimated from historical catch records. We describe a technique by which growth information can be extracted from otoliths of long-lived species such as Sebastes through sectioning and careful measurement. As an example, data from recently collected Sebastes diploproa and S. pinniger are used to describe growth at ages 1 through 6 during several decades of this century. We describe the technique and its limitations, and make suggestions for application of the resulting data.

Introduction

The study of long-term changes in marine fish populations has recently received a great deal of attention. Understanding the responses of fish populations to physical and biotic variability can lead to predictive capability; indeed, many current studies in fisheries oceanography examine the causes of past population change with the goal of modeling future trends in populations. Obviously such information can be most useful for purposes of fisheries management.

Several categories of long-term change in marine fish populations have been investigated. Population or stock size has generally been estimated from historical catch records of fisheries, and data from many decades are available, as for some Pacific salmonid stocks (Mysak et al. 1982) and several North Atlantic fisheries (Cushing 1982). Species assemblages and biotic interactions have been described on the decade scale by current work of the California Cooperative Oceanic

Fisheries Investigations (Loeb et al. 1983; H. G. Moser, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92038 pers. commun.), and on the century scale by Soutar and Isaacs (1974) for the same region.

Methods of data collection for developing time series either come from continuous data collection or extraction of naturally stored information. The former often occurs over generations of biologists. Since starting a new series may not allow achievement of objectives for 30 or more years, available time series (which are often collected for other purposes) are used. In some cases, however, naturally stored information can be used to extract historical population information. A classic example of this approach is the study of cycles of population abundance for *Engraulis*, *Sardinops*, and *Merluccius* by Soutar and Isaacs (1974). By measuring the abundance of scales in anoxic sediments, they were able to define natural cycles of abundance of these species for 150 yr. Information is also stored in the otoliths of individual fish (Radtke 1984). The study of age in fishes and the use of otoliths for back calculation are simple examples of extraction of historical information, and others have used isotopic composition to define thermal habitats occupied by individual fish (Mulcahy et al. 1979).

The study of growth in fishes has typically been concerned with relatively short-term growth of cohorts or populations, most often with fished stocks. Differences in growth may exist between stocks (Templeman and Squires 1956; Borisov 1979), geographical regions (Boehlert and Kappenman 1980), and among years (Margetts and Holt 1948). Such growth differences may be genetically based (Borisov 1979), the result of density dependence (Margetts and Holt 1948), or caused by several environmental factors, most importantly temperature (Brett 1979). Unfortunately, comparisons of growth with time often come from different studies, frequently made difficult by changes in sampling, ageing methodology, or interpretation (Boehlert and Kappenman 1980).

Because estimates of fish growth are generally made at a single point in time, time series on the order of several decades do not exist for any species. Since otoliths act as recording chronometers, however (Radtke 1984; Campana and Neilson 1985), back calculation techniques allow one to establish growth patterns early in the life history of fishes, even in older fish. Extreme longevity has recently been confirmed in the scorpaenid genus *Sebastes* (Bennett et al. 1982), and ages in excess of 80 yr have been reported for several species (Archibald et al. 1981; Boehlert and Yoklavich 1984; Leaman and Beamish 1984). Thus otoliths of these species hold the potential to derive estimates of growth from several decades ago. In this paper we describe a modification of back calculation techniques, from which historical growth patterns can be obtained, and we apply this technique to two species, the splitnose rockfish, *Sebastes diploproa*, and the canary rockfish, *S. pinniger*.

Materials and Methods

Otolith samples were collected during rockfish surveys conducted by the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, during 1977 (Boehlert 1980), 1980 (Boehlert and

Yoklavich 1984), and 1983 (Wilson 1985). Collection techniques followed Gunderson and Sample (1980). Since one objective was to represent as many years of growth as possible, we based otolith selection upon age alone; old fish in this study thus greatly outweigh their relative abundance in a random sample. Otoliths were sectioned and age determined as outlined in Boehlert and Yoklavich (1984).

Back calculations and measurement of growth increments were limited to the first 6 yr of growth. This limit was imposed because otolith increments become smaller with increasing age; eventually, linear growth stops and the otolith begins to thicken (Bennett et al. 1982; Boehlert 1985). We used two different techniques for otolith measurement. For _S. diploproa_, whose otoliths are typically more opaque and increments smaller, we measured from dorsal to ventral distal edges of annuli 1-6. In the faster-growing _S. pinniger_, in which otoliths are clearer, we measured from the focus to the dorsal distal edge of each increment (Fig. 1).

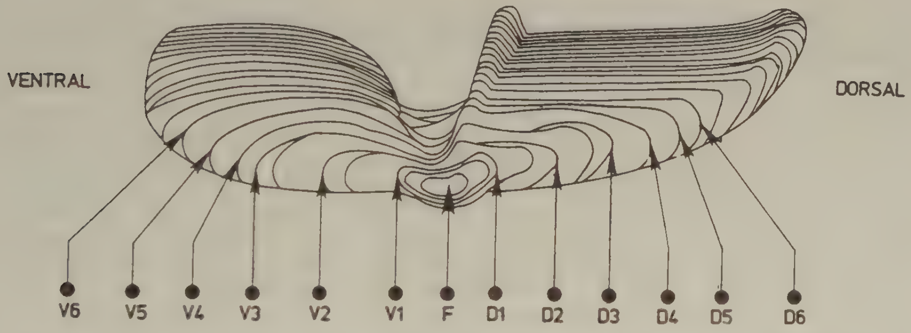

Figure 1. Schematic drawing of an otolith section from _Sebastes_ showing the axes of measurement used in the current study. Measurements for _S. diploproa_ were from dorsal to ventral distal margins (i.e., V2 to D2); measurements used for _S. pinniger_ were from focus to dorsal distal margin) (i.e., F to D2).

Data analysis and interpretation

Available data included sex, length, date of collection, location information, total age, and widths of the measured annuli for ages 1-6. The growth increment (GI(I), where I = 1 to 6, determined by subtraction of measurements of adjacent annuli rather than the full measurement), was used so that growth in a given year was not cumulative and therefore did not reflect past growth. Age was subtracted from year of collection to determine the year of birth. For each fish, each growth increment (1-6) was associated with a specific "year of growth." Data on 6 yr of growth were therefore available for each fish with the exception of those younger than six at the time of sampling. As an example, a fish collected in 1980 and aged as 40 yr was born in 1940; growth measurements from this individual were therefore available for years 1940 through 1945. Table 1 demonstrates a subset of the data array available for this series.

Table 1. A subset of the data array for growth increments used in the present study. The numbers under growth increment represent the years of birth for these growth years. The first growth increment is defined to occur in the year of birth, the second growth increment in the following year, and so forth.

Growth year	Growth increment, GI					
	1	2	3	4	5	6
1940	1940	1939	1938	1937	1936	1935
1941	1941	1940	1939	1938	1937	1936
1942	1942	1941	1940	1939	1938	1937
1943	1943	1942	1941	1940	1939	1938
1944	1944	1943	1942	1941	1940	1939
1945	1945	1944	1943	1942	1941	1940
1946	1946	1945	1944	1943	1942	1941

The majority of specimens used in the study were males. To increase the sample size, however, otoliths were collected from both males and females. Since growth, particularly after sexual maturity, differs between sexes for these two species (Boehlert and Kappenman 1980), it was necessary to test for differences in the growth measurements to allow a combination of growth data from males and females independent of the years tested. We separated the data by sex and then aggregated the data for each growth increment such that each year of birth had a single, mean value. Differences in growth between sexes were tested by comparing the respective growth increments with a paired t-test for all years where both male and female data were available. The results of this test showed that no differences were evident between sexes for either species.

Yearly means of GI(I)'s were calculated and these were the values upon which further calculations were made. A long-term average and standard deviation were calculated for each series of yearly mean growth increments and the standardized growth anomalies A(I) were calculated as follows:

$$A(I) = \frac{[GI(I) - (\text{mean } GI(I))]}{(\text{SD } GI(I))}$$

These anomalies have a mean of zero and a standard deviation of one, allowing comparison of the growth anomalies in different growth years without concern for the effects of growth increment magnitude. Comparisons between species would also be facilitated by this conversion.

Results and Discussion

A total of 802 *S. diploproa* (651 males and 151 females) and 942 *S. pinniger* (616 males and 326 females) were used in this study. The *S. diploproa* ranged in age from 1 to 86 yr and had a birth date distribution from 1896 to 1979 (Fig. 2A). Specimens of *S. pinniger* ranged in age from 2 to 60 yr and had a corresponding birth date

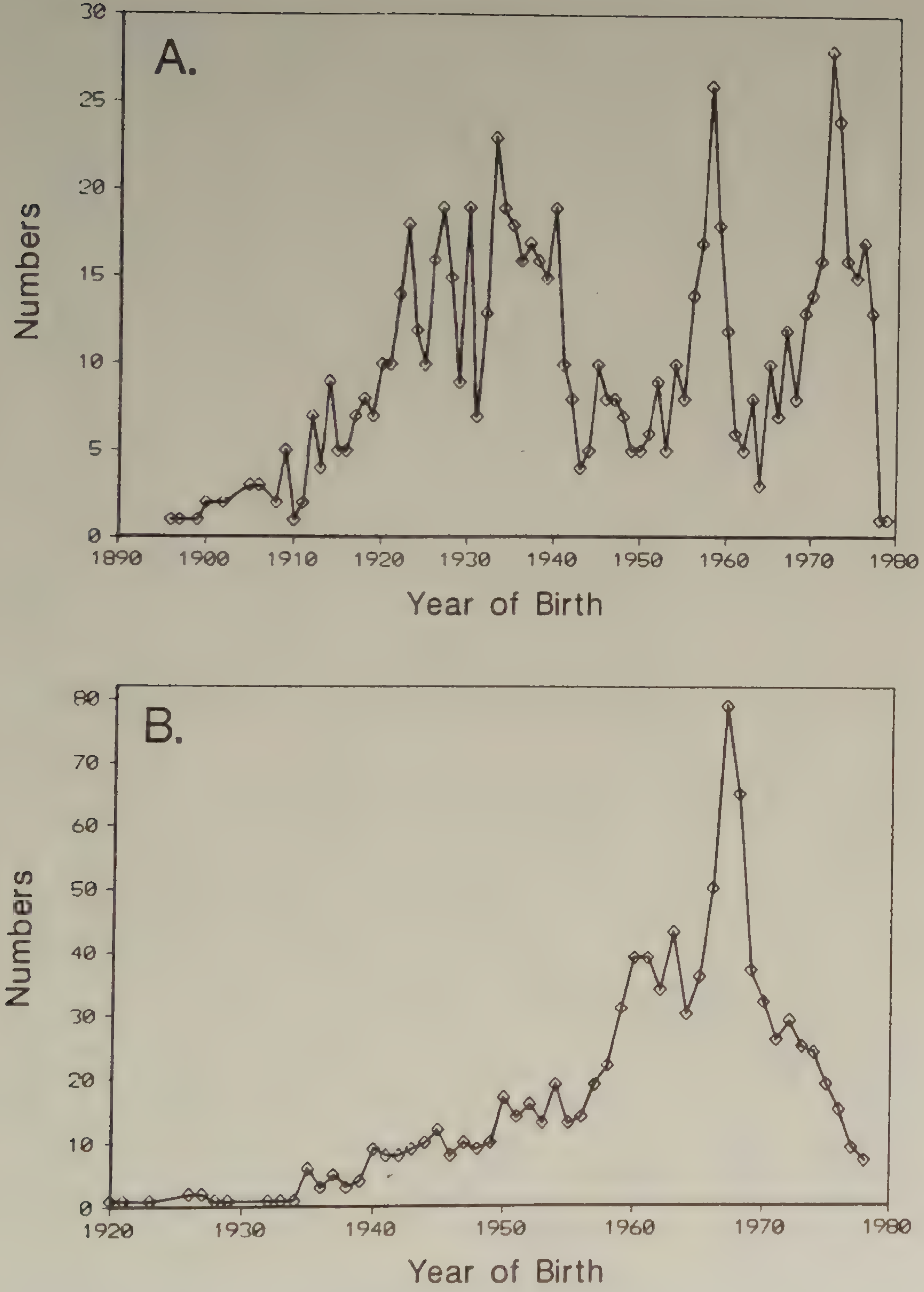

Figure 2. Distribution of the years of birth of specimens used in the present study. Males and females are combined. A. *Sebastes diploproa*. B. *S. pinniger*.

distribution from 1920 to 1978 (Fig. 2B). The total numbers of growth increments available were 4,714 for *S. diploproa* and 5,600 for *S. pinniger*. In the discussion of the results to follow, several sources of error contribute to the variability of these results. From a methodological standpoint, three errors are quickly apparent. First, minor changes in the location of the section of the otolith (Fig. 1) may result in slightly different increment measurements; we expect this to introduce relatively minor errors, however, since the sectioning technique (Boehlert and Yoklavich 1984) was consistent throughout the study. The second source of error occurs in the estimate of total age. Errors in this estimate will result in assignment of the incorrect year of birth and subsequent years of growth for each growth increment (Table 1). Finally, errors in annulus selection while making measurements on the section can occur. None of these errors are expected to be systematic, however, and their cumulative effects should not significantly mask trends in the data.

A concern from a biological standpoint is the implicit assumption that there is no linkage of longevity and growth. That is, if long-lived individuals are characterized by either faster or slower growth rates during the first 6 yr of life than individuals with shorter lifespans, we can encounter problems when comparing young with old fishes. A genetic basis for such a difference in growth and age at sexual maturity has been suggested for cod (Borisov 1979). An investigation into the biochemical genetics of *S. diploproa* using electrophoresis at 29 loci showed no variation associated with age (Wishard and Boehlert, unpubl. data). Although negative results cannot rule out a difference, our growth results do not show a consistent trend which would support a genetic basis for growth differences.

As one would expect from growth data, there is definite variability in the growth anomalies for both species (Figs. 3,4). No clear trends in either faster or slower growth over the full time series are apparent for either species. The 5-yr running averages, however, show an interesting pattern. In *S. diploproa* (Fig. 3), most of the age classes show a trend of positive anomalies before about 1925, and negative anomalies from about 1955 to 1970; positive anomalies after 1970 are also apparent in most of the records. The relationships among the age classes are also of interest. Generally, there is a relationship among anomalies 2-6 for this species, but the anomaly for year 1 is uncorrelated with growth in any other year. *Sebastes diploproa* is a deeper living member of this genus as adults, but the first year is spent in surface waters (Boehlert 1977); thus the factors which are important in growth in the first year may differ from those which determine growth in subsequent years. Temperature, which can have an important impact on juvenile rockfish growth (see summary in Boehlert and Yoklavich 1983), may differ between deep and shallow water (Kruse and Huyer 1983).

For *S. pinniger*, the record is somewhat shorter but shows interesting trends (Fig. 4). For age classes 1-4, there appears to be a positive anomaly through about 1952 followed by a period of negative growth until about 1970. Age classes 5 and 6, however, seem to show the opposite trend during these periods. All age classes show concordance, however, in the pattern of positive anomalies after about 1970. This same trend, although much weaker, was observed for *S. diploproa* (Fig. 3).

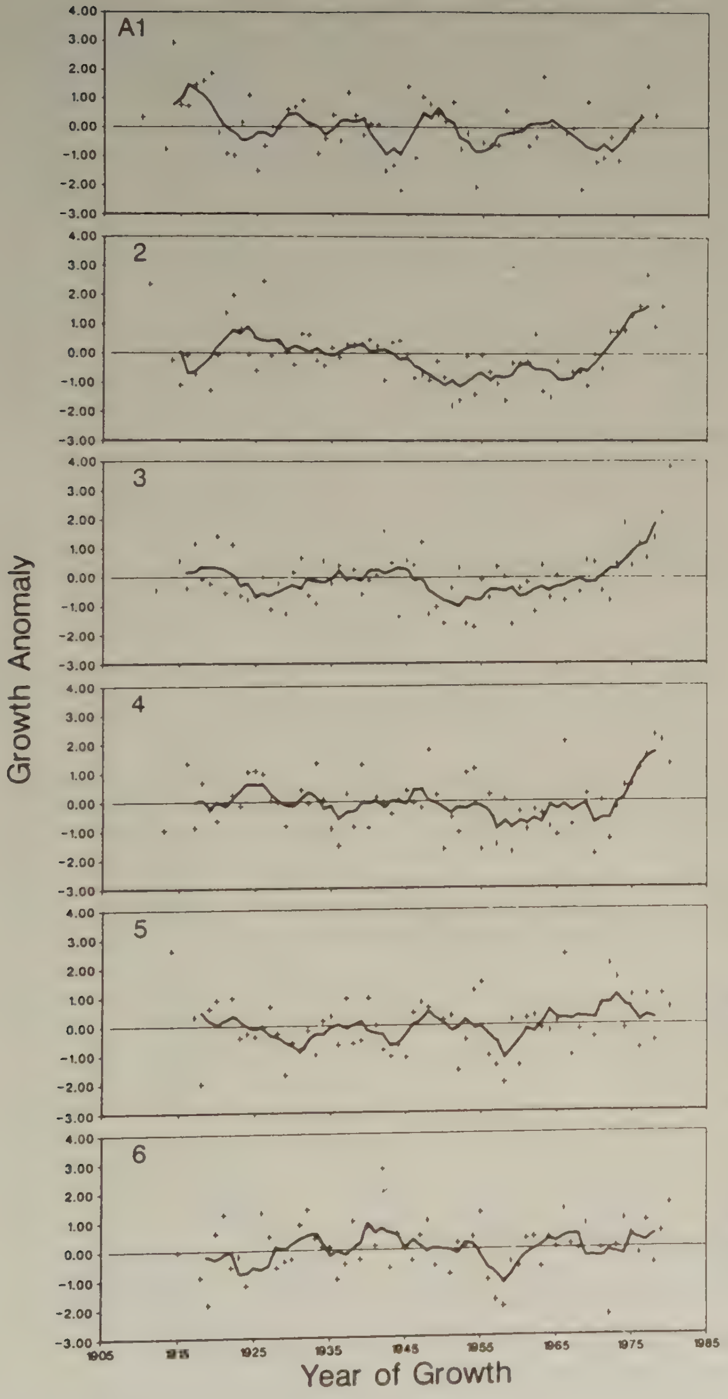

Figure 3. Plot of growth anomalies in years of growth 1-6 for *Sebastes diploproa*. The data points represent the yearly growth anomalies. The curve represents the 5-yr running average of these data. Only years where mean growth increment was based upon four or more observations were used in these figures.

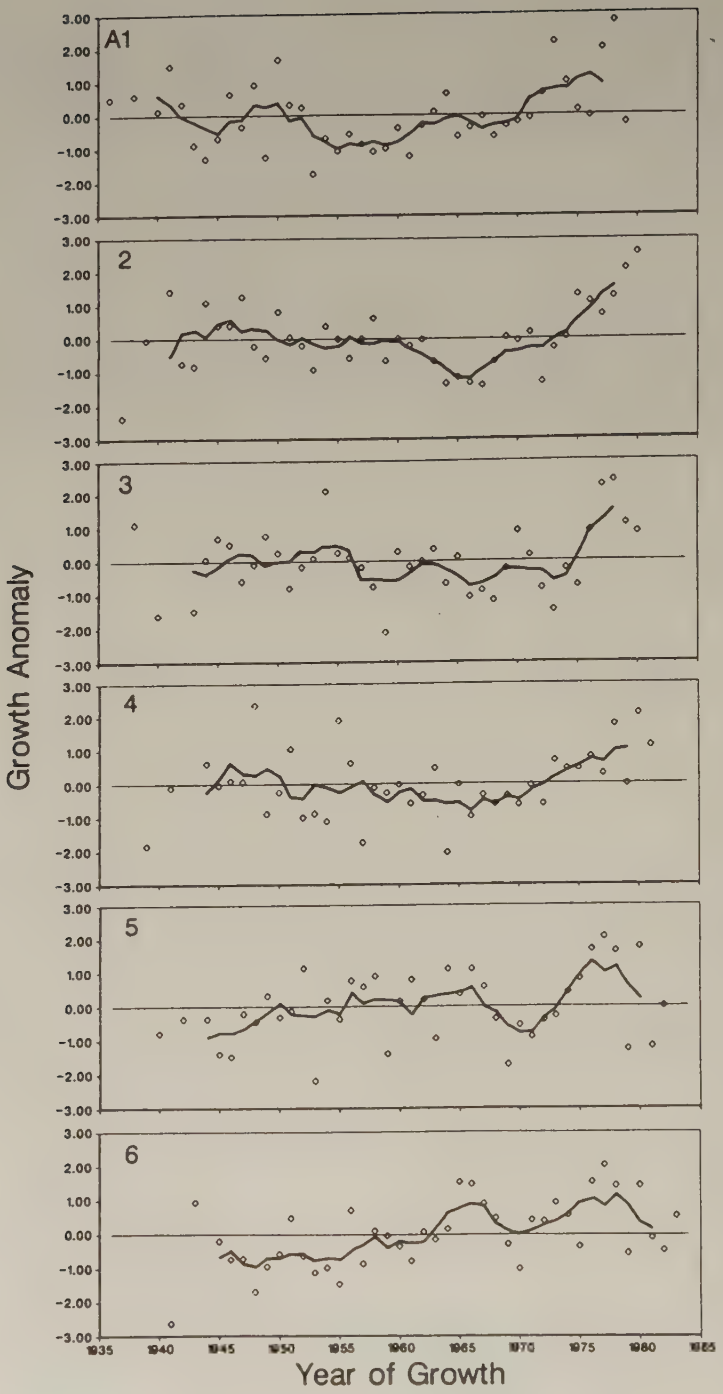

Figure 4. Plot of growth anomalies in years of growth 1-6 for *Sebastes pinniger*. The data points represent the yearly growth anomalies. The curve represents the 5-yr running average of these data. Only years where mean growth increment was based upon four or more observations were used in these figures.

The technique which we describe in this paper allows development of time series of growth for long-lived species of fishes. The results we have presented for these two species will need further statistical analysis to discern trends in the data and to investigate the possible sources of variation in growth patterns. For example, time series analysis may show relationships with physical factors, as described by Chelton et al. (1982) and Mysak (1986). Biological causes for growth variation may also be implicated. In this regard, it is significant that the apparent increase in growth after 1970 (Figs. 3,4) is temporally related to the depletion of coastal stocks of _Sebastes_ as described by several papers in this volume. Does this hint at density dependent growth patterns? Future research on this data base will address these questions.

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A study of delayed capture mortality syndrome in skipjack tuna, *Katsuwonus pelamis* (L).

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Abstract. This study was initiated to determine the cause(s) of delayed mortality in newly captured skipjack tuna, *Katsuwonus pelamis* (L.), being held at the National Marine Fisheries Service Kewalo Research Facility. Sixty-four per cent of 244 skipjack tuna delivered to the facility died, usually on the second or third day after capture. The capture history, morphological data, serum chemistry (21 standard parameters), haematology, and histological samples of major organs, were obtained from 30 fish sampled at sea immediately after capture, or after approximately 4, 9, 24, 48 or 500+ h in captivity. The cause(s) of death in these fish could not be attributed to anoxia, disseminated intravascular coagulation, lactic acidosis, capture myopathy or infection. Post-capture haemodilution is hypothesized as a major factor of delayed capture mortality syndrome in skipjack tuna.

Introduction

The capture and maintenance of large marine fish is necessary for public aquaria display, aquaculture or scientific study. The capture and transport of a large fish is a difficult and expensive task which too often results in the death of the fish. The stress of capture and adaptation to captivity initiates complex physiological responses by the fish which appear to lead to dysfunction in organ systems resulting in death (Love 1970; Mazeaud, Mazeaud & Donaldson 1977). The initial stress of capture has been reported to cause almost immediate death in wild mammals from simple trauma, shock (i.e. low blood pressure) and subsequent pooling of blood (Soma, Burrows & Marshal 1974). Capture-related deaths in fish have been attributed to anoxia (Hall 1930; Pawson & Lockwood 1980) or lactic acidosis (Black 1958; Beamish 1966; Wardle 1978). Delayed mortalities following capture in fish have been attributed to disseminated intravascular coagulation (Smith 1980), loss of osmotic homeostasis (Stevens 1972; Pic, Mayer-Gustan & Maetz 1974, 1975; Eddy 1981; Pawson & Lockwood 1980; Sleet & Weber 1982), muscle myopathy and renal tubular necrosis (Roberts, McQueen, Shearer & Young 1973; Harthoorn & Young 1974), or secondary bacterial or viral infection (Mazeaud *et al.* 1977). Studies by Beggs, Holeton & Crossman

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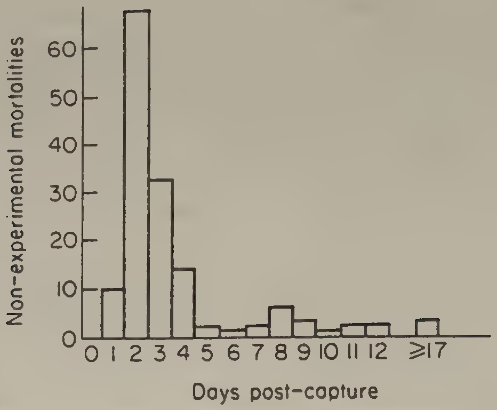

Figure 1. Incidence of mortalities of 244 live-caught skipjack tuna after arrival at the Kewalo Research Facility.

Clinical observations

After transfer to the 24-ft holding tanks the fish usually, but not always, formed a loosely organized school. On the first day after capture, swimming speed, judged by following the schooling fish around the tank perimeter, was greater than that of capture-adapted tuna and the tuna made frequent sharp turns. When not swimming as a school in a circular pattern around the perimeter of the tank, a common swimming pattern was a 'figure eight'. Tuna swimming in a figure eight pattern would do so along 6 m of tank wall shaded from the slanting rays of the sun. The radius of turn at the ends of the figure eight was approximately 1 m. This turn was sharp enough that the fish often lost forward momentum at the apex, necessitating a burst of tail beats to regain cruising speed. Within 2 days, tuna of questionable health were seen swimming very close to the circumferential tank walls, often scraping the sides of their bodies against the vinyl liner of the tank. These fish lacked a visual response to objects in or above the water, tended not to school with other fish in the tank, and were usually found dead within a day of showing the 'wall scraping' behaviour.

By contrast, tuna that adapted to captivity had a more relaxed random swimming pattern and formed a tight, well-coordinated school within the tank. Adapted tuna were constantly changing the frequency of their tail beat by alternating a series of moderate tail beats with short periods of coasting or gliding when tail movement was minimal.

Therefore, the clinical signs associated with postcapture mortality included: (1) increased swimming speed, (2) absence or reduced use of coast and glide swimming behaviour, (3) 'figure eight' swimming patterns, (4) scraping along the sides of the tank, and (5) collapse and death, usually on the second or third day after capture.

Gross lesions

The weight–length ratios of the 4 h (n=7) and 500+ h (n=2) (capture-adapted) fish, were close to the normal weight described by the weight–length equation for skipjack tuna (Nakamura & Uchiyama 1966). The weight–length ratio of fish 24 and 49 h after capture

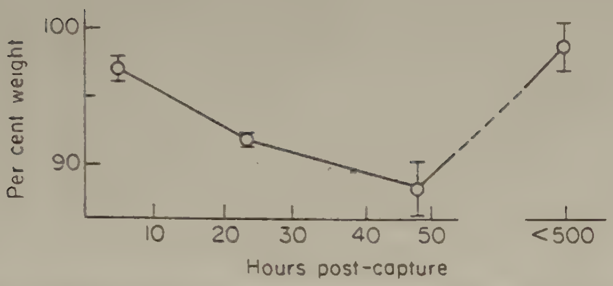

Figure 2. Weight of fish expressed as percentage of 'normal' weight from length–weight regression (mean ± sem).

averaged 92 and 89% of normal indicating a weight loss of approximately 10% (180 g) after being delivered to the holding tanks (Fig. 2).

Gross lesions on fish found dead in the tanks included scrape marks along the flanks and corneal opacity of the eyes. These lesions were probably a result of the 'wall scraping' behaviour described above. Occasionally a tuna was observed with hook injury involving

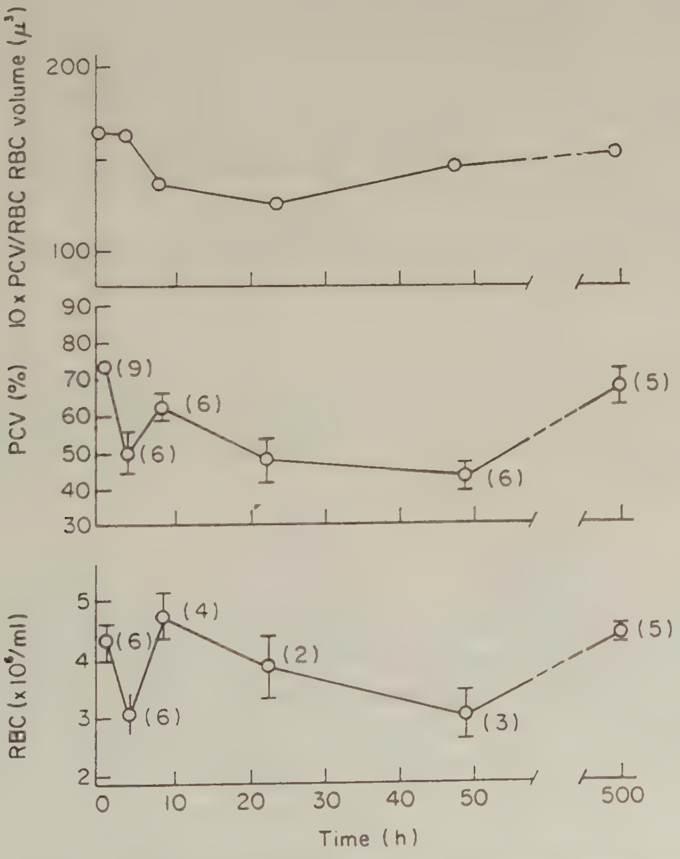

Figure 3. Haematology. Changes in (a) mean red blood cell volume (10×PCV/RBC), (b) packed cell volume (PCV%), and (c) mean red blood cell count (RBC×10^6/ml), up to 500 h post-capture (all values ± sem).

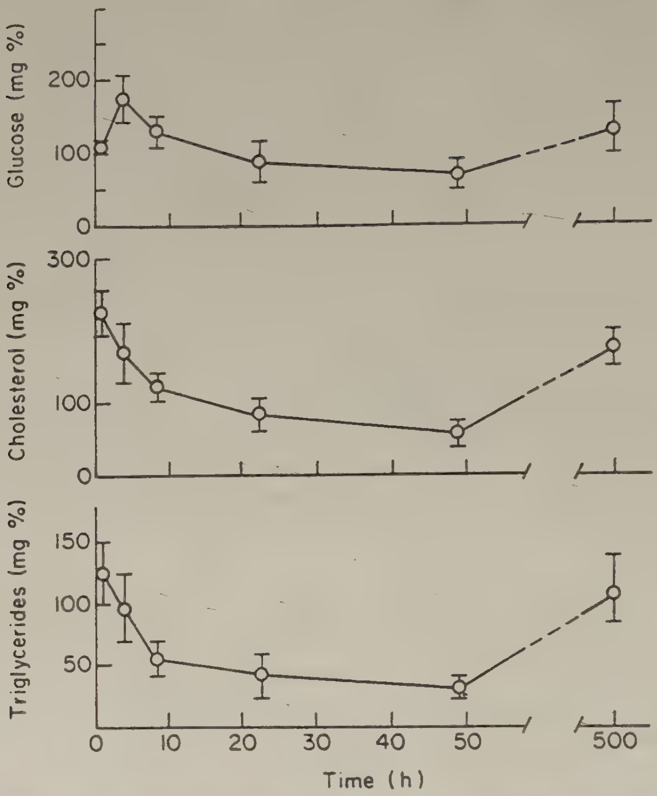

Figure 4. Changes in serum glucose (mg %), cholesterol (mg %), and triglyceride levels (mg %) in fish up to 500 h post-capture (mean ± sem).

tearing or dislocation of bones in the upper jaw; however, the barbless hook usually caused only minor injuries which were difficult to find during postmortem examination.

The upper intestine and lower portions of the stomach of all tuna examined were infected with digenean and nematode parasites.

Haematology

Packed cell volume averaged 74% in tuna sampled at sea, but decreased sharply within 4 h to 46% and returned to near basal levels (63%) at 9 h. Red blood cell count followed the same pattern as PCV but did not decrease proportionally as much as did the PCV, thereby causing an apparent decrease in the mean red blood cell volume (PCV*10/RBC) (Fig. 3). Although not specifically measured, it was noted that the time required for clot formation within the plain blood tubes varied widely between individual fish.

Serum chemistry

Cholesterol, glucose, triglycerides, proteins, calcium, iron and lactic acid were generally lower in fish killed during the first 48 h after capture but were near basal levels in capture-

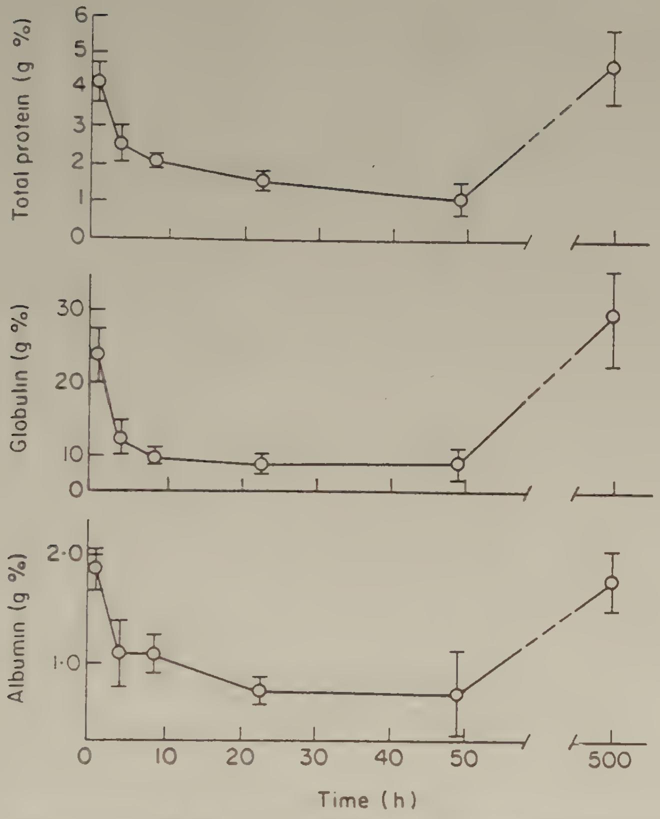

Figure 5. Serum proteins: total protein (g %), globulin (g %), and albumin (g %) in tuna up to 500 h post-capture (mean ± sem).

Table 1. Summary of changes (± sem) in variables associated with delayed capture mortality syndrome (DCMS) in captive skipjack tuna. Basal values are from wild-caught fish at sea. The DCMS values are from fish in captivity for 20–60 h. Capture adapted values are from two fish (except as noted) in captivity for at least 500 h

Parameter	Basal	DCMS	Capture adapted
Weight (% normal) (n=5)	0·970±0·011	0·916±0·010	0·99±0·024
Packed cell value (%) (n=5)	71·9±3·4	44·8±3·3	62±4·5
Red blood cell count ($\times 10^6$/ml)	173±33	135±14	177±4
Total protein (g %)	4·2±0·55	1·7±0·25	3·8, 5·8
Albumin (g %)	1·87±0·18	0·76±0·15	1·5, 2·1
Cholesterol (mg %)	221±35	68±12	150, 201
Triglycerides (mg %)	124±27	34±5·4	79, 139
Osmolarity (mOs)	447±13	360±18	377, 424
Calcium (mg %)	19·8±2·1	12·1±1·4	16·8, 20·3
Iron (mg %)	140±24	30·5±9·6	131, 122
Chloride (meg/l)	171±1·7	185±3·8	160, 165
Lactate (mg %)	117±6	69±15	31, 46
Glucose (mg %)	109±3·3	75±15	164, 97

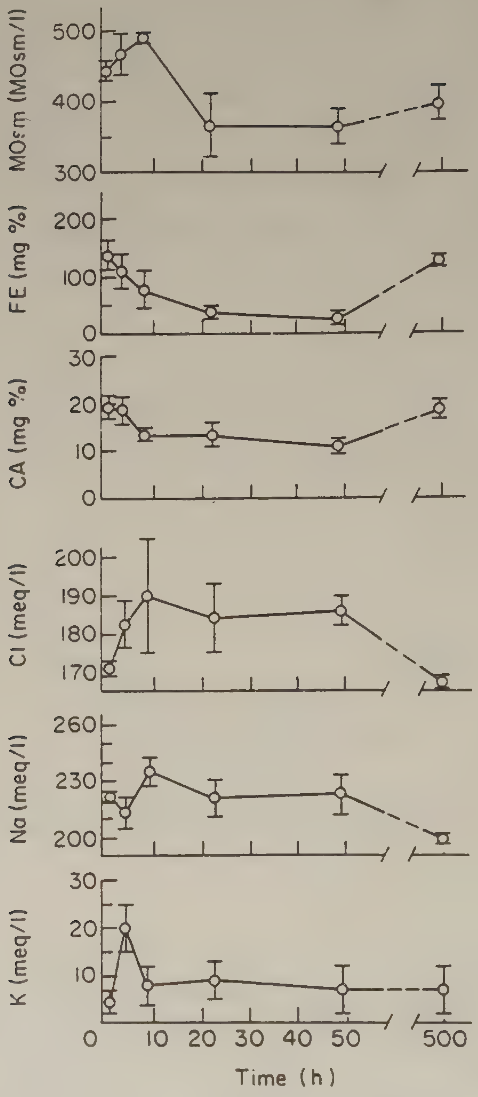

Figure 6. Measure of (a) total serum osmolarity (MOsm/l) and the major serum electrolytes, (b) iron (FE mg %), (c) calcium (CA mg %), (d) chloride (meq/l), (e) sodium (NA meq/l), and potassium (K meq/l) in the serum of tuna up to 500 h post-capture (mean ± sem).

adapted (500+ h) tuna (Figs 4–6 & Table 1). Serum enzymes decreased from initially high levels and remained low in capture-adapted animals (Fig. 7). Only uric acid and plasma chloride levels increased significantly during the first 48 h after capture (Fig. 8 & Table 1). The BUN, creatinine, alkaline phosphatase and bilirubin did not show significant changes (Figs 5–8 & Table 1).

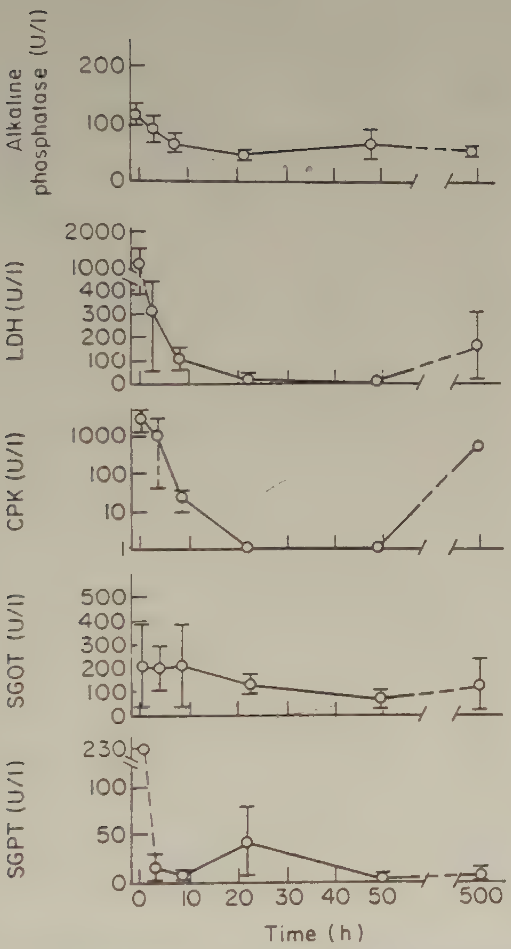

Figure 7. Serum enzyme levels: alkaline phosphatase (U/l), LDH (U/l), CPK (U/l), SGOT (U/l), and SGPT (U/l) (mean ± sem).

Histology

Mild congestion of caudal kidney, liver and other visceral organs was observed in DCMS tuna as compared to basal or capture-adapted fish. Focal acute degeneration of muscle cells was seen in three, two, and one muscle fibres, respectively, in three of six DCMS fish sampled from the 48 h group. No other microscopic morpho-anatomical differences were found between DCMS tuna and basal or capture-adapted tunas.

Discussion

The primary response exhibited by the skipjack tuna to capture and handling was similar to the stress response described for other marine fish. There were transient increases in blood

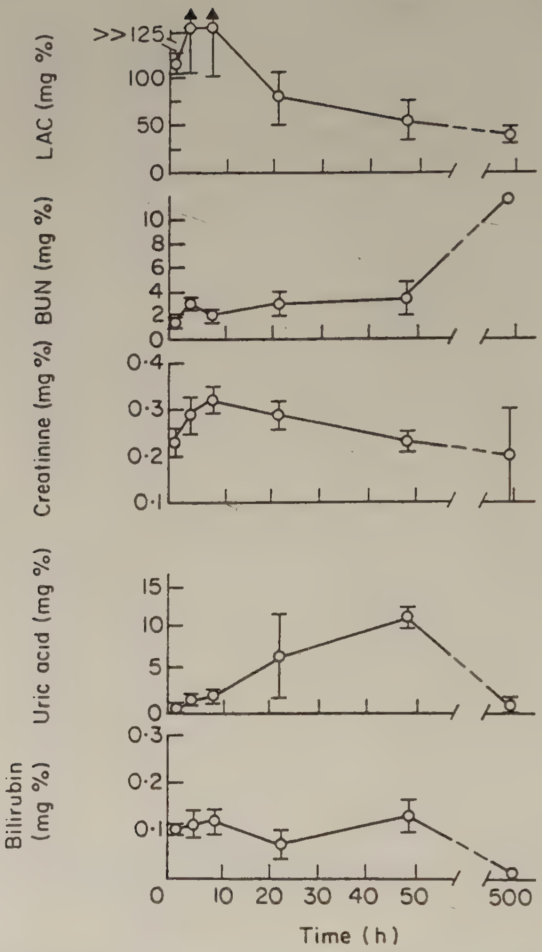

Figure 8. Metabolic waste products: (a) Serum lactate (LAC mg %), (b) blood urea nitrogen (BUN mg %), (c) creatinine (mg %), (d) uric acid (mg %), (d) bilirubin (mg %), were measured up to 500 h post-capture (mean ± sem).

glucose and lactate levels after capture. There was a transient increase in serum osmolarity due primarily to an increase in the major blood ions, chloride, lactate and potassium. There was an approximate 10% weight loss from fish held in captivity for 9–49 h (Fig. 3). The majority of mortalities occurred 24–48 h after capture.

It is unlikely that the observed mortalities were caused by simple trauma. There were no obvious scrape marks or hook wounds on the fish used in this study which would have debilitated the fish. Observations by R. W. Brill (Southwest Fisheries Center Honolulu Laboratory, NMFS, Honolulu) and R. Kearney (South Pacific Tuna Commission, Noumea, New Caledonia, personal communication) at the Kewalo Research Facility indicate that skipjack tuna adapted to captivity have a very low mortality rate as a result of recapture by hook, tagging and release back into their holding tank.

The evidence does not support the hypothesis that death was due to either anoxia, or bacterial or viral infection. The high incidence of mortalities after 24–48 h in captivity occurred too late to be caused by anoxia and too soon to be caused by infection. Histological examination failed to find evidence supporting infection as a cause of death. Similarly, death caused by lactic acidosis cannot be established. Even though the blood levels of lactate reached extremely high concentrations approximately 4–8 h after capture, the deaths did not occur until 48 h after capture, at which time the blood lactate levels were significantly reduced.

Signs usually associated with capture myopathy, including weakness, impaired or noncognizant vision, incoordination, and death following severe physical stress (Harthoorn & Young 1974), were all apparent in captured skipjack tuna. However, clinical pathologic abnormalities, such as an elevation in circulating enzymes (SGOT, CPK, LAD, SGPT; Fig. 7) indicative of muscle sarcomere damage and kidney lesions often associated with capture myopathy in mammals, were not found in these fish during the period of mortality. Therefore, the data do not support the hypothesis that the fish died from capture myopathy.

Also, disseminated intravascular coagulation (DIC) does not appear to be the cause of death. Although some pooling or intravascular coagulation of blood may have occurred (as evidenced by the 'congestion' noted during histological examination), there was no evidence of haemorrhage, blood clots, or the presence of distorted or damaged red blood cells which are indicative of DIC. Further, although DIC has been suggested as a possible cause of death (Smith 1980), it has never been demonstrated in fish.

Osmotic dysfunction did occur during the first 8 h after capture. Sodium, chloride, potassium, iron and calcium normally constitute the major contributors to serum osmolarity (MOsm/l), but other molecules such as serum proteins or lactate ions may contribute significantly if they occur in abnormally high concentrations. The transient increase in serum osmolarity (Fig. 6) appears to be due primarily to the increase in chloride, lactate and potassium. Increased corticosteroid levels effect active ion transport across the gills and decrease water uptake through the intestinal epithelium (Pic *et al.* 1975; Eddy 1981), possibly causing an increased serum ion level accompanied by dehydration. An increased drinking rate and subsequent absorption of ions and water across the gastroesophageal membrane, as described by Sleet & Weber (1982) for buffalo sculpin, would presumably lead to increased serum ion levels accompanied by hydration. The apparent 10% weight loss in fish from the 23- and 49-h groups suggests that the tuna were losing water and gaining salts across the gills without adequate replenishment by swallowing water. The high serum osmolarity and ion levels were only transitory. Concentrations at or below basal levels were observed within 24 h of capture, a full 24 h before the majority of mortalities occurred.

Haemodilution could explain the almost equivalent drop in total protein, globulin, albumin, triglycerides and cholesterol, all of which decreased 58–63% from basal levels within 24 h of capture. Calcium decreased 30% and iron 71% in the same period. The parallel decreases in these values make it likely that the cause was dilution. The PCV, often used as an indicator of haemodilution in mammals, decreased 'only' 36% during the first 24 h. However, release of erythrocytes from the spleen and kidneys could account for the discrepancy between the percentage dilution suggested by PCV decrease (36%) and the decrease suggested by other serum chemistry values (60%).

The blood volume of fish may not be as stable as that of land vertebrates. Alexander &

Ingram (1980) noted that the PCV of an immobilized albacore decreased during the first 12 h but forwarded no hypothesis as to the reason for this decrease. Harbell, Hodgins & Schiewe (1979) noted a decrease in PCV, total protein, albumin, globulin, chloride, sodium, total osmolarity and alkaline phosphatase levels, and the presence of a distended gut filled with fluid in juvenile freshwater salmon experimentally infected with vibriosis. The infected fish gained weight and the control fish actually lost weight during the experiment. They ascribed the low plasma protein and osmolarity to kidney failure. Osmolarity changes and haemodilution similar to those found in this study have been observed in anaesthesized buffalo sculpin (Sleet & Weber 1982). These authors attribute the serum dilution to factors other than fluid uptake across the upper gastrointestinal tract.

The source of the fluid that increases the blood volume is unknown. It is tempting to attribute the rapid rise in blood osmolarity and increased volume to the fish swallowing and absorbing water and salts from the gut faster than the ion-exchange mechanism in the gills can excrete the added salt load. Assuming an average normal blood volume of 6% in a 1·8 kg skipjack tuna, approximately 130 ml of diluting fluid would be required to dilute the blood by 60%. However, the addition of only 1·5 ml of sea water ([Cl]=1900 mg/dl) would be adequate to account for the observed 11% increase in the serum chloride concentration, but considering the apparent weight loss of 10% during the first 48 h in captivity and the results of Sleet & Weber, it seems more plausible that the diluting fluid came at least partially from the more isotonic inter- or intracellular tissue fluids and was then lost to the surrounding sea water by osmosis.

Although the initial function of haemodilution could be to maintain blood pressure and adequate blood flow, thereby keeping the fish alive, excessive haemodilution could cause death due to several factors including: (1) inability to control acid-base balance due to low serum proteins, (2) decrease in the oxygen and metabolite carrying capacity of the blood, or (3) impairment of metabolite transfer through tissue membranes. The authors hypothesize that delayed capture mortality syndrome (DCMS) is caused by the combined effects of several factors including haemodilution, tissue dehydration and excessive fluid weight loss. Further experiments are needed to test this hypothesis; for instance, measurement of the internal water and electrolyte balances in the different body compartments and in the environment.

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Seasonal and Interannual Subsurface Temperature Variability off Peru, 1952 to 1984

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Abstract

Time series of monthly means of subsurface ocean temperature data along the Peru coast are developed for the period 1952 to 1984 for historical studies of anchoveta populations. Monthly mean values of sea surface temperature (SST), depth of the 14°C isotherm, and thickness and heat content of the surface layer were computed from all available subsurface temperature profiles. Means of these four parameters were computed for five areas along the Peru coast from 1 to 17°S, extending approximately 300 km offshore. Intra-annual (seasonal) and interannual variations of the four parameters are described and plotted as contour isograms. Time series of the four parameters are presented for the region from 4 to 14°S, as are monthly means of the Southern Oscillation Index and SST and sea level at Talara and La Punta (Callao), Peru.

Introduction

The coastal waters off the west coast of South America, particularly off Peru, are among the most biologically productive regions of the world's oceans (Ryther et al. 1971). The Peruvian anchoveta *(Engraulis ringens)* once supported the world's largest fishery. The high productivity of the area is a result of coastal upwelling which is an oceanic response to the southeasterly trade winds which cause offshore Ekman divergence, elevating the thermocline and bringing relatively cold, nutrient-rich water to the euphotic zone where the nutrients can be utilized by phytoplankton photosynthesis (Barber et al. 1985). The upwelling ecosystem off Peru is subject to considerable natural variability, with prominent time scales ranging from days to decades. This paper examines two temporal scales of oceanic variability which are likely to affect populations of anchoveta: seasonal (months) and interannual (years). The seasonal or intra-annual variability, being strongly dependent upon the annual solar cycle, is relatively predictable, and therefore likely to promote evolutionary adaptation (Parrish et al. 1983; Bakun, this vol.). The interannual variability, by contrast, has an irregular period which would tend to promote population variations. The dominant form of interannual variability off Peru occurs when the normal seasonal upwelling of nutrients is interrupted by "El Niño" intrusions of relatively warm, clear oceanic waters from the west and north.

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The coastal upwelling off Peru is imbedded within the Peru current system, which consists of several more or less independent currents interacting in a rather complicated manner (Wyrtki 1966). Gunther (1936) first distinguished a poleward countercurrent situated between the northwestward flowing Peru Coastal Current and the northwestward flowing Peru Oceanic Current farther offshore. This intermediate current, the Peru Countercurrent or Gunther Current, is a weak and irregular southward flow along 80°W and is usually observed only as a subsurface current. At the surface it is usually concealed by the wind drift to the northwest and west. It is strongest near 100 m depth, but reaches to about 500 m.

According to Wyrtki (1965, 1966), the Peru Coastal Current flows northwestward along the coast with velocities of 10-15 cm/s. At about 15°S, much of this flow turns westward away from the coast and increases speed to 25-35 cm/s as it joins the South Equatorial Current. Generally, the Peru Coastal Current is strongest from April to September. North of 15°S, the wind drift remains northwestward, but it is shallow and the southward flow of the Peru Undercurrent lies immediately beneath the shallow surface layer. The combined system of the Peru Coastal Current, the westwardwind drift, and the subsurface Peru Countercurrent maintain the upwelling along the coast. North of 15°S, the upwelling is supplied by equatorial subsurface water which is of high salinity and low oxygen content and flows southward in the Peru Countercurrent. The Peru Oceanic Current, which flows in a more westward direction and is slightly stronger than the Peru Coastal Current, seems to have little direct interaction with the more complicated processes closer to the coast.

The mean topography of the thermal structure of the Eastern Tropical Pacific reflects the ocean currents and has been described by Wyrtki (1966). The thermocline is relatively shallow along the coast at depths of 40 to 60 m and slopes downward in the offshore direction to depths of over 200 m about 1,000 km offshore. A region of shallow thermocline extends westward from the coast along the equator out to 130°W and beyond.

The current system off Peru is related to the large-scale oceanic and atmospheric circulations over the entire tropical Pacific. The atmospheric circulation over the region is dominated by the Hadley circulation of rising air over the equatorial region and sinking air over mid-latitudes near 30°N and 30°S. The Hadley circulation creates the high-pressure systems observed over the oceans in these latitudes which are strongest in the summer and weakest in the winter of their respective hemispheres. The meridional Hadley circulation is modified by zonal Walker circulation of rising air over the warm western tropical Pacific (WTP) and sinking air over the cold, upwelled water of the eastern tropical Pacific (ETP). The zonal Walker circulation normally causes heavy rainfall and low pressure over the WTP and sparse rainfall and high pressure over the ETP. The trade winds result from the combination of the Hadley and Walker circulations: the trades blow equatorward from the mid-latitude oceanic highs toward the lower pressure at the equator and westward from the higher pressure over the ETP to the lower presure over the WTP.

The surface wind stress created by the northeast and southeast trade winds drive the warm surface water westward in the North and South Equatorial Currents, respectively. This westward transport of mass and heat depresses the thermal structure and raises the sea level in the WTP. By conservation of mass, the high sea level in the WTP requires a poleward flow of the western boundary currents of the North and South Pacific gyres and eastward flow in the North and South Equatorial Countercurrents and the equatorial Undercurrent or Cromwell Current (within a degree or so of the equator).

The zonal slope of the sea surface downward from the high sea levels in the WTP to the lower sea levels in the ETP establishes a reverse zonal slope of the thermocline upward from the WTP to the shallow thermocline of the ETP. Meyers (1979) showed that near the equator (between 1°N and 1°S), the 14°C isotherm varies from depths of 200 to 250 m in the WTP to depths of 100 to 150 m in the ETP. Off the South American coast, local alongshore winds induce offshore Ekman divergence and the associated upwelling. This upwelling elevates the relatively shallow thermocline, bringing nutrient-rich deep water to the euphotic zone where it supports a high level of biological productivity. In addition, the trade winds cause oceanic divergence or surface transport away from the equator. This divergence forces local upwelling along the equator, which produces a region of shallow thermocline and above normal productivity that extends westward along the equator from the coast.

Interannual variations of the stength of the trade winds cause changes in the ocean circulation and related changes in the upwelling of nutrients off Peru. According to the hypothesis of Wyrtki (1975), El Niño occurs when a weakening or reversal of the trades occurs after a sustained period of anomalously strong trades. The period of stronger than normal winds forces an even greater than normal east to west slope of the sea surface. When the trade winds slacken or reverse, the forcing of the higher than normal sea levels in the WTP is removed. This imbalance generates equatorially-trapped baroclinic disturbances which propagate eastward along the equator in the form of equatorial Kelvin waves (Enfield and Allen 1980). The propagation of these long-period internal waves, and the associated energy, across the entire equatorial Pacific from Indonesia to South America has been observed using an extensive array of sea level monitoring stations (Wyrtki and Nakahara 1984). Upon encountering the South American coast, this energy is observed as a large intrusion of warm water which depresses the normally shallow thermocline and causes a rapid rise in sea level along the coast. As a result, normally arid regions of Peru and Ecuador receive inordinate amounts of rain, with severe flooding occurring during major events.

Interannual variations in the strength of the trade winds are part of a global pattern of surface pressure variation called the Southern Oscillation. The Southern Oscillation is often measured by the difference of atmospheric pressure between weather stations in the ETP and WTP. Quinn (1974) and Quinn and Neal (1983) have used the difference of atmospheric pressure between Easter Island (representative of the Indonesian low) as an index of the Southern Oscillation (SOI, see Table 1). Quinn (1974) demonstrated the strong relationship between anomalously low SOI values and the occurrence of El Niño off the coasts of Peru and Ecuador. A time series of anomaly of the SOI pressure difference shows the major El Niño events of recent decades (Figs. 1 and 2). Note the strong positive SOI presure differences (and implied strong trade winds) during 1954-1956 and 1970-1971. Subsequent sharp declines in the SOI pressure difference in the winters of 1956-1957 and 1971-1972 were followed by El Niño events, as evidenced by the increased SST and sea level at Talara and La Punta. Also, note that the strong 1982-1983 El Niño was not preceded by a period of strong positive SOI, rather, it occurred during a period of predominantly negative SOI which began in 1976.

The formation of El Niño has been modelled numerically by McCreary (1976) who suggested that the anomalous deepening of the density structure observed during El Niño events dissipates by reflection in the form of westward propagating baroclinic Rossby waves and transmission to the north and south along the coast as low-frequency coastally trapped waves and coastal Kelvin waves. Such baroclinic waves can be observed as anomalous deepenings of temperature and salinity surfaces adjacent to the coast and as anomalous rises of sea level at coastal tide stations. Poleward currents along the coast are created in geostrophic response to the anomalous deepening and change in slope of the density surfaces normal to the coast. The currents reverse to equatorward as the anomalous deepening dissipates. To some extent these processes occur each year and anomalous warm years are merely an extreme condition of the normal annual cycle of events (Chavez et al. 1984).

Although the interannual changes associated with El Niño events are dominant, longer period fluctuations also occur. In their 34-year time series of temperature at 100 m along the west coast from British Columbia to Chile, Brainard and McLain (1985) showed a marked warming trend occurring between the early and late 1950s, cooling in the 1960s, and warming again in the mid-1970s and early 1980s (see also Tables 2 and 3). The causes of these long-term temperature trends are unknown, but like the interannual variations, they are related to changes in both the large-scale atmospheric and oceanic circulations. The period of below normal SOI pressure differences during the years 1976-1983 (Fig. 2) is an example. El Niño-like conditions of above normal SST and sea level occurred during much of this period in the northeast Pacific (McLain 1983, and see Fig. 2 and Tables 4 and 5 for monthly sea level data from 1950 to 1974).

Development of historical time series of subsurface temperature conditions off Peru is important for modelling historical changes in fish populations of the area. This paper presents plots and tables of monthly mean values of four parameters computed from subsurface temperature observations for 1952 to 1984 for use in historical studies. These four parameters are SST, depth of the 14°C isotherm, depth to the temperature that is 2.0°C less than the surface temperature (SST-2°C), and heat content from the surface to the SST-2°C isotherm. The depth

Table 1. Southern Oscillation Index (SOI). Monthly mean pressure difference in millibars between Easter Island and Darwin, Australia. Data courtesy of Dr. W. Quinn, Oregon State University.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1948	12.9	11.7	12.3	10.4	9.3	11.6	10.7	11.2	9.3	12.1	9.8	9.3
1949	8.0	12.8	15.0	6.2	7.8	11.9	10.3	9.7	11.7	11.3	13.4	15.1
1950	16.4	17.6	15.0	14.7	9.5	13.8	11.3	9.2	9.1	16.0	17.1	17.6
1951	14.3	14.3	12.9	7.3	4.1	7.8	4.6	5.2	5.4	9.9	13.6	11.8
1952	13.2	11.5	10.8	5.5	8.6	7.0	10.9	8.9	5.8	11.6	12.8	11.3
1953	12.6	9.1	12.1	8.3	6.1	8.4	6.7	5.0	8.2	16.2	12.8	12.8
1954	15.4	15.2	10.6	11.0	10.7	7.1	11.0	8.6	13.8	15.3	14.9	16.3
1955	11.2	18.6	13.9	13.2	10.9	10.6	10.0	11.7	16.2	16.8	13.3	15.1
1956	15.9	15.3	13.6	12.3	12.7	8.0	9.1	10.5	10.7	11.8	10.5	9.8
1957	10.2	10.8	10.0	7.7	3.9	4.1	7.0	8.6	8.6	11.8	9.4	11.5
1958	11.0	13.4	11.3	6.1	3.4	10.3	2.9	10.8	8.6	12.0	13.4	8.5
1959	15.0	11.1	10.1	11.7	5.5	10.0	5.9	11.3	8.5	11.2	13.8	14.5
1960	11.0	12.5	9.4	9.1	8.3	5.4	9.3	9.7	12.5	12.7	12.6	10.5
1961	12.3	14.9	9.5	13.0	4.8	4.4	1.6	4.0	10.0	10.1	11.5	12.0
1962	12.4	11.1	10.6	10.2	10.6	7.5	7.3	11.0	13.0	14.2	10.6	13.2
1963	16.2	13.5	14.9	8.2	5.0	6.0	11.9	7.9	7.5	7.7	12.9	10.6
1964	12.3	13.0	13.0	11.1	6.4	9.9	8.7	11.2	13.1	10.3	9.5	12.8
1965	12.5	12.9	10.1	8.0	4.5	3.2	3.2	6.3	6.7	11.3	8.3	10.2
1966	10.5	13.7	10.4	7.8	3.3	10.4	5.0	10.3	12.0	10.4	11.1	13.8
1967	14.3	15.5	12.7	6.3	9.1	11.6	13.9	11.0	12.5	10.7	11.0	12.5
1968	15.9	12.9	14.8	8.3	7.5	10.8	8.3	6.3	4.8	12.0	10.2	12.7
1969	10.2	14.7	12.7	7.1	6.0	6.3	3.5	8.6	8.2	10.5	15.9	13.1
1970	12.8	12.8	9.8	7.0	12.4	10.2	10.2	10.0	11.9	13.3	16.5	16.8
1971	15.5	16.0	15.2	11.2	14.3	11.1	5.2	12.0	12.7	11.3	14.5	15.1
1972	10.4	11.5	13.4	7.5	.6	.3	5.5	3.2	4.8	8.2	10.2	8.9
1973	12.5	12.7	13.0	8.9	7.6	9.5	8.4	10.7	13.6	13.0	16.2	16.5
1974	16.8	17.1	15.4	9.5	6.1	10.1	9.4	5.3	11.2	13.4	15.7	13.0
1975	11.6	8.6	13.8	8.7	3.8	8.6	8.8	13.4	13.3	14.0	13.6	14.9
1976	14.5	15.0	13.7	6.7	2.4	3.5	3.1	8.2	5.2	7.2	11.0	7.6
1977	10.2	15.0	8.0	5.3	2.3	5.9	11.1	10.0	4.8	7.0	11.5	10.5
1978	13.1	9.7	9.6	6.0	7.8	9.1	7.6	10.7	10.3	6.9	9.1	11.6
1979	11.0	13.1	10.9	4.5	3.7	9.7	2.7	1.1	9.2	10.1	8.3	9.9
1980	13.6	12.2	9.4	8.6	7.4	7.5	6.6	7.3	6.5	12.4	10.3	10.5
1981	16.5	15.0	8.0	7.3	7.6	6.4	8.0	7.4	6.2	9.5	13.6	13.2
1982	14.2	14.4	12.2	4.2	6.3	6.9	2.9	1.5	4.0	6.8	5.3	7.2
1983	3.9	4.3	7.3	7.2	5.8	6.4	4.6	9.0	10.9	10.5	12.4	10.5
1984	9.9	13.6	10.9	5.6	7.0	6.6	8.4	6.5	6.5	10.6	12.5	14.2
1985	13.1	14.2	13.4	12.7	8.3	4.8	5.9	13.0	10.1	****	****	****

of the SST-2°C isotherm indicates the thickness of the mixed layer which provides a measure of the depth of the thermocline and hence, relates to upwelling and availability of nutrients to the euphotic zone. This definition of mixed layer is similar to that used by Robinson and Bauer (1976), except that they chose the depth that is 2°F (1.1°C) less than the SST. The SST-2°C depth was selected for defining the depth of the thermocline from smooth average temperatures because 2°C is larger than the small positive and negative temperature changes near the surface that are present in both the raw data and the analyzed values. Also, a temperature change of 2°C is large enough to reach the large gradients found in the thermocline.

The 14°C isotherm is at depths of 80 to 180 m off Peru and is below the strongest gradients of the thermocline. Variations in the depth of the 14°C isotherm are indicators of large-scale vertical movements of the water column, such as upwelling. Also, Barilotti et al. (1984) related the depth of the 14°C isotherm off San Diego, California, to the depth of the thermocline and hence to the supply of nutrients for kelp growth.

Heat content down to SST-2°C is an indicator of the overall environmental change in the euphotic zone. Combined with wind-derived Ekman transports (Bakun, this vol.; Mendo, this vol.), these vertical temperature parameters can be used to describe the offshore velocity structure which is critical to the reproductive success of the anchoveta (Parrish et al. 1983, and other contributions in this vol.).

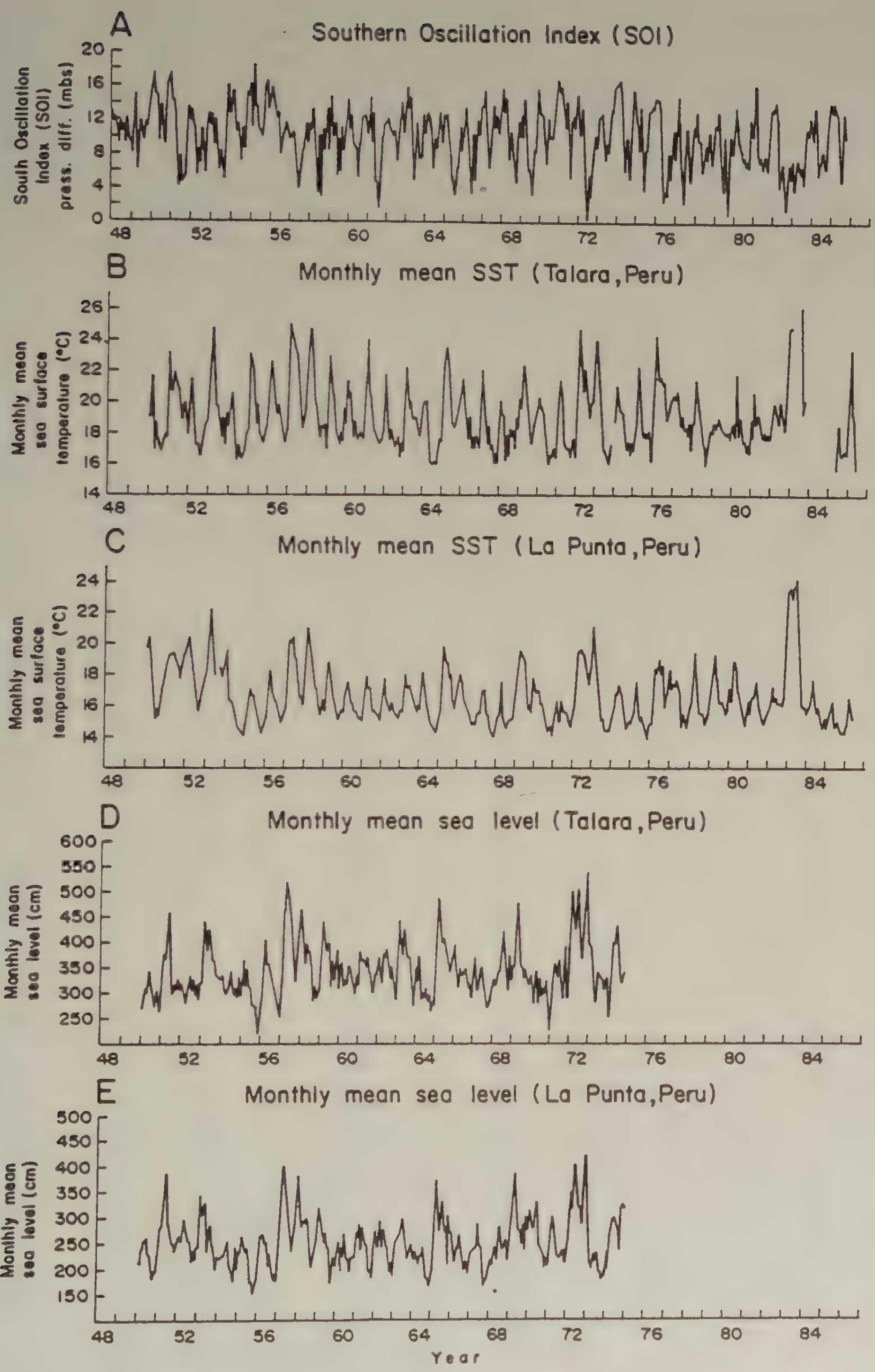


Fig. 1. Time series of monthly means of (A) Southern Oscillation Index (difference of surface barometric pressure in millibars between Easter Island and Darwin, Australia), (B and C) SST in degrees C, and (D and E) sea level in cm at Talara and La Punta, Peru. Values are computed as monthly means of daily observations.

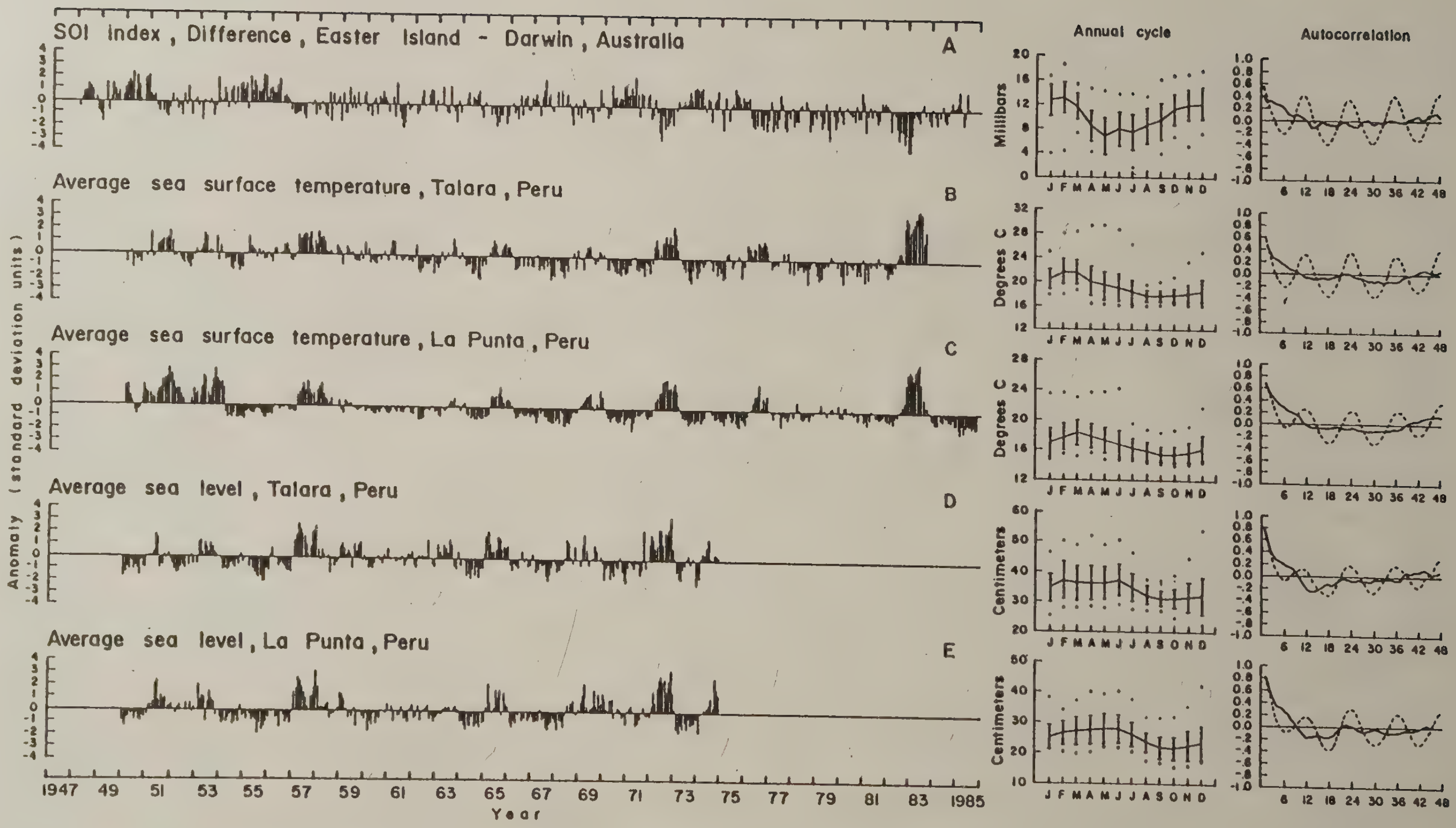
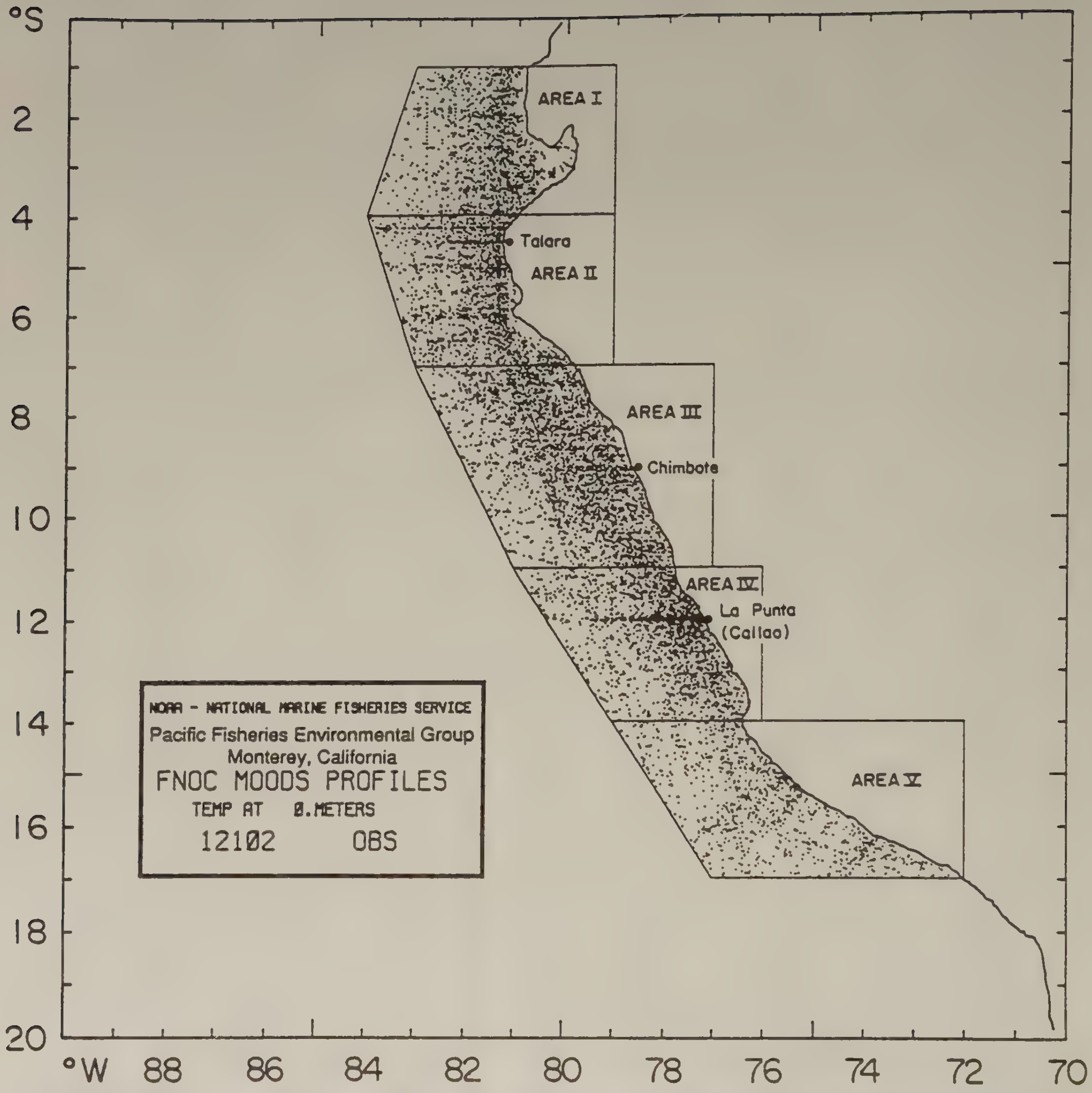


Fig. 2. Annual cycles, autocorrelation functions, and anomalies of monthly means of daily observations at coastal and island stations. Parameters are (A) Southern Oscillation Index, (B and C) SST, and (D and E) sea level at Talara and La Punta, Peru. The annual cycle plot (center) shows the long term (1943-1986) monthly means, between-year standard deviations (bars), and range of interannual variability (dots). The autocorrelation function plot (right) shows the autocorrelation of each original data series (dotted) and the autocorrelation of each anomaly series (solid). The time series of anomalies from 1941-1986 mean (left) are shown in standard deviation units for intercomparison between data series. Based on data in Tables 1-5.

Mean values of the four parameters were computed for each month for the 33-year period from 1952 to 1984 for five areas along the coast from 1 to 17°S (Fig. 3). Each of the given areas spanned 3 degrees of latitude except for the central-most area which spanned 4 degrees. The zonal extent of each area was chosen so that they would extend about the same distance offshore, roughly 300 km. In addition, all data prior to 1952 were combined to form a single composite year. Thus, the resulting fields of monthly means for each parameter for the 5 areas covers 34 years (408 months), for a total of 2,040 cells. The average value for the region from 4 to 14°S was obtained by averaging the values computed for the three central areas. Mean temperature at 25 m depth intervals from the surface to 350 m were also computed for the central area to show vertical variations of temperature with time. The data are plotted as contour isograms of latitude (area) or depth *vs.* month to show both seasonal and interannual variations.

Table 2. Monthly mean sea surface temperature in degrees Celsius at Talara, Peru. Data courtesy of Dr. D. Enfield, Oregon State University.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1950	19.0	21.6	21.7	16.9	18.6	17.6	17.3	16.8	17.6	17.9	17.7	18.1
1951	23.2	20.6	20.9	21.9	21.4	21.1	20.5	18.8	18.9	19.8	19.6	17.9
1952	19.8	21.4	20.6	18.4	17.2	17.3	16.5	16.5	17.1	17.7	18.6	18.8
1953	20.8	23.0	24.8	23.6	19.7	19.7	18.8	17.7	19.0	17.2	19.2	18.4
1954	19.5	20.6	20.4	17.2	16.2	17.1	16.4	16.3	16.7	16.7	17.9	18.2
1955	22.8	22.9	22.4	20.9	18.6	19.7	18.0	17.8	17.3	17.4	18.3	17.9
1956	19.2	22.6	22.5	20.3	19.5	19.3	19.8	18.5	18.1	17.4	17.4	17.9
1957	20.7	25.1	24.3	23.9	23.4	22.8	21.0	19.4	18.3	19.1	19.4	22.1
1958	22.8	24.8	23.8	21.0	19.9	19.7	18.2	17.7	18.4	18.4	18.6	17.0
1959	20.3	23.0	22.4	20.6	19.9	18.1	17.5	17.2	18.0	17.5	19.6	18.6
1960	21.3	20.3	20.6	18.7	17.7	18.7	17.6	17.7	18.0	17.8	17.6	19.6
1961	22.4	24.1	20.7	20.1	18.9	18.1	17.8	17.6	17.3	17.5	17.5	18.1
1962	21.8	19.3	18.7	17.6	18.2	17.5	17.1	17.3	17.8	16.4	17.2	16.8
1963	19.4	22.3	20.8	19.6	19.9	18.9	19.0	19.0	18.4	17.8	17.9	19.2
1964	20.1	19.9	20.1	18.5	16.1	16.0	16.1	16.0	16.0	17.0	17.6	17.5
1965	20.3	22.5	23.3	23.5	22.0	19.8	18.6	18.3	18.5	19.1	19.4	20.2
1966	21.2	21.5	19.4	17.9	17.6	19.1	17.0	17.7	17.0	17.8	17.2	17.1
1967	20.5	22.1	19.4	18.5	17.3	18.4	16.9	17.1	16.1	16.4	16.1	18.1
1968	20.1	19.3	19.1	16.2	17.9	16.6	18.3	17.8	18.1	17.0	19.0	18.4
1969	20.2	19.7	22.4	22.3	21.6	19.7	18.2	17.3	17.5	18.4	18.8	19.2
1970	20.3	19.8	19.6	19.3	18.0	16.8	16.0	16.5	16.5	17.0	16.5	16.5
1971	19.5	20.5	21.5	20.5	17.5	17.0	17.0	17.0	16.5	17.5	17.5	16.5
1972	19.8	23.9	24.8	22.3	20.7	22.2	21.0	19.5	19.0	19.9	20.1	23.3
1973	24.0	23.6	21.9	19.4	17.9	16.9	16.7	16.2	16.0	17.0	17.3	16.0
1974	18.8	21.2	20.4	19.5	19.4	19.1	18.0	16.9	17.4	16.6	17.4	16.9
1975	17.8	18.6	22.4	21.5	19.8	17.8	18.0	17.7	18.1	18.1	16.2	17.7
1976	20.5	24.4	23.6	21.4	21.7	21.2	21.2	19.0	18.9	19.5	20.1	20.3
1977	20.5	20.3	20.8	19.4	18.5	19.1	18.2	18.3	17.9	18.7	16.9	18.7
1978	18.7	21.5	20.1	19.1	18.6	17.3	17.2	15.9	17.3	17.8	18.2	18.1
1979	18.7	18.3	18.7	19.0	18.7	18.3	18.2	18.1	17.9	18.0	17.6	18.5
1980	18.6	17.8	21.8	17.8	19.0	18.4	17.4	17.5	16.8	17.2	16.7	18.9
1981	17.7	20.7	18.6	19.2	19.1	18.7	17.7	18.0	17.6	17.9	17.7	17.7
1982	18.4	19.9	19.9	19.6	18.7	20.0	20.0	18.5	18.2	20.9	23.4	24.9
1983	24.9	27.9	28.3	29.2	29.2	28.5	26.2	19.3	20.1	****	****	****
1984	****	****	****	****	****	****	****	****	****	****	****	****
1985	****	****	****	****	15.7	18.6	17.0	16.6	16.7	16.9	16.7	18.6
1986	20.2	23.5	19.4	18.8	15.7	****	****	****	****	****	****	****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AREA I
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AREA III
AREA IV
AREA V
Talara
Chimbote
La Punta
(Callao)
NOAA - NATIONAL MARINE FISHERIES SERVICE
Pacific Fisheries Environmental Group
Monterey, California
FNOC MOODS PROFILES
TEMP AT 0.METERS
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Fig. 3. Locations of five areas along the Peru coast for which subsurface temperature profiles were extracted from the FNOC MOODS and used to perform analyses of surface and subsurface temperature. A total of 12,102 profiles were extracted from the MOODS files for all five areas for SST analyses. Area I is the northernmost area and Area V, the southernmost.

Table 3. Monthly mean sea surface temperature in degrees Celsius at La Punta, Peru. Data courtesy of Dr. D. Enfield, Oregon State University.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1950	19.8	20.4	19.6	18.3	16.3	15.1	15.6	15.4	16.3	17.2	17.2	17.9
1951	18.7	18.9	19.3	19.3	19.4	19.2	18.9	18.5	17.7	18.7	19.2	19.2
1952	19.5	20.0	20.4	19.2	18.1	16.7	16.0	15.7	15.9	16.8	16.9	17.9
1953	18.2	20.3	22.3	21.5	19.0	18.0	****	****	18.4	17.8	18.3	19.2
1954	19.6	16.3	16.4	16.2	15.5	15.2	14.7	14.5	14.4	14.2	14.1	15.2
1955	15.9	16.5	17.1	16.7	16.6	15.9	15.6	15.0	14.4	14.2	14.7	15.1
1956	15.4	17.2	18.2	17.8	16.7	16.5	16.0	15.8	15.3	14.9	15.2	15.5
1957	15.9	19.2	20.2	20.0	20.4	19.1	18.9	17.5	16.5	16.6	16.1	18.3
1958	19.9	21.0	20.0	18.9	18.1	17.3	17.1	15.9	15.5	15.4	16.4	15.7
1959	15.8	18.4	18.8	18.1	17.7	16.5	16.0	15.5	15.2	15.2	15.7	15.6
1960	16.7	17.2	17.6	16.9	16.2	16.1	15.6	15.6	15.4	15.1	15.2	15.0
1961	16.2	17.6	17.9	17.1	17.2	15.9	15.6	15.7	15.5	15.4	15.1	15.3
1962	16.8	17.8	16.5	16.1	15.7	16.3	16.0	15.6	15.5	15.4	15.2	15.7
1963	15.6	16.3	18.1	17.3	17.1	17.3	16.9	16.5	16.2	15.6	15.9	15.8
1964	17.3	18.2	17.3	16.7	15.8	15.4	14.9	14.7	14.6	14.3	14.5	14.9
1965	15.4	16.5	19.9	19.6	18.9	18.6	17.8	18.0	16.4	15.9	16.6	17.4
1966	17.9	18.1	17.6	16.5	16.1	15.9	15.6	15.1	14.8	14.9	14.8	15.4
1967	15.6	15.5	17.0	17.0	17.0	15.5	15.3	14.6	14.3	14.0	14.1	14.6
1968	15.3	15.4	17.6	15.5	14.9	14.6	14.6	15.0	15.1	15.1	15.4	16.4
1969	17.4	18.6	19.5	19.6	19.2	19.1	16.7	15.8	15.9	15.6	17.8	17.8
1970	16.9	17.0	17.0	16.1	16.1	15.6	15.0	14.5	14.4	14.7	14.1	14.8
1971	15.5	16.3	15.1	16.0	16.3	15.8	15.6	15.5	15.3	14.8	14.8	15.3
1972	16.0	17.6	19.5	19.5	19.7	19.4	19.3	18.8	17.9	17.4	18.2	19.0
1973	21.1	20.5	19.0	17.4	16.2	15.1	15.2	14.4	14.4	14.4	14.4	14.8
1974	15.3	15.8	16.8	16.8	17.3	16.9	16.3	15.5	14.7	14.6	15.0	14.9
1975	15.3	15.6	17.2	17.6	16.6	15.1	15.3	14.7	14.2	13.9	14.8	14.9
1976	14.8	16.9	18.4	18.2	18.5	19.0	18.1	18.6	15.9	16.6	16.9	18.3
1977	17.1	17.4	17.3	17.7	17.2	16.6	14.6	15.5	15.0	14.6	15.3	15.6
1978	16.2	17.7	19.5	18.1	16.5	15.6	15.5	15.5	14.8	15.1	15.5	16.2
1979	17.0	17.8	19.4	17.9	17.6	16.2	16.2	16.2	15.8	15.5	15.7	17.2
1980	16.3	16.9	18.9	18.6	17.3	16.7	16.4	15.6	15.3	14.7	15.7	16.3
1981	15.5	16.6	16.5	16.8	17.6	16.7	15.7	15.4	14.9	14.9	15.3	15.5
1982	15.6	16.3	17.3	16.4	16.6	16.2	16.2	16.2	16.0	16.5	19.0	21.7
1983	23.5	23.6	23.0	23.7	23.8	24.2	19.6	17.4	16.0	16.0	15.9	15.5
1984	15.8	16.1	16.7	17.9	16.4	15.6	15.8	15.5	14.8	14.6	15.2	14.7
1985	15.1	15.5	15.5	16.3	14.7	14.7	15.0	14.7	14.3	14.3	14.2	14.3
1986	14.7	16.6	15.9	15.3	15.2	****	****	****	****	****	****	****

Data Acquisition and Processing

Data Sources

The profiles of subsurface temperature for the Peru coastal region were acquired from the US Navy Fleet Numerical Oceanography Center (FNOC) in Monterey, California. The profiles were obtained by merchant, naval and research vessels of many nations using a variety of sampling instruments, including bottle casts, mechanical bathythermographs (MBT), expendable bathythermographs (XBT) and electronic conductivity/temperature/depth profiles (CTD). The capability and accuracy of these instruments vary widely: MBTs, with typical accuracies of 0.3 to 1.0°C, were used until the development of XBTs in the 1960s. Generally, MBTs reached depths of only 100-200 m, whereas the newer XBTs are capable of depths to 450, 700, or even 1,500 m. The accuracy of XBTs are typically 0.1 to 0.4°C. Bottle casts and CTD casts from research vessels are capable of any depth, with typical cast depths to 1,000 or 1,500 m and accuracies of 0.001 to 0.1°C. Profiles from all of these sources are normally mailed to oceanographic data centers and assembled into common data sets. The time lag between observation and final assembly of the data by the data centers may be 5 to 10 years or longer. To reduce this time lag, many of the profiles are manually digitized and transmitted by radio in near

Table 4. Monthly mean sea level (cm) at Talara, Peru. Data courtesy of Dr. D. Enfield, Oregon State University.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1950	267	287	310	301	342	318	310	294	275	303	272	264
1951	344	373	366	386	460	450	303	301	317	307	328	307
1952	315	302	281	291	312	333	303	325	295	317	285	318
1953	316	442	431	383	425	412	363	358	334	327	326	323
1954	333	305	301	300	310	342	313	297	307	292	329	294
1955	339	363	314	346	310	308	276	274	272	249	219	260
1956	293	383	402	357	356	335	323	306	295	280	263	247
1957	342	455	471	519	487	471	426	357	321	343	420	455
1958	463	410	355	395	381	377	354	285	311	292	298	311
1959	385	442	407	382	394	393	312	358	326	349	380	309
1960	354	354	312	323	317	352	351	329	309	299	333	316
1961	380	365	362	366	351	370	341	330	300	305	336	339
1962	371	336	319	377	369	386	355	327	352	314	295	286
1963	343	442	394	376	425	417	369	369	344	293	275	351
1964	322	373	356	286	299	291	309	282	297	264	279	274
1965	368	486	487	432	397	407	385	379	357	340	367	379
1966	395	342	310	343	336	337	345	344	310	317	291	292
1967	364	367	303	318	347	350	330	282	269	274	285	312
1968	328	313	317	338	344	379	421	369	320	306	374	327
1969	351	343	434	478	411	351	348	330	344	337	317	331
1970	334	278	328	341	281	328	292	307	299	322	273	226
1971	260	333	355	347	331	364	336	289	294	392	289	327
1972	412	501	461	427	436	505	463	367	374	384	445	539
1973	397	386	309	285	281	341	335	330	325	306	330	321
1974	254	284	376	400	396	431	427	333	318	332	341	343

Table 5. Monthly mean sea level (cm) at La Punta, Peru. Data courtesy of Dr. D. Enfield, Oregon State University.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1950	212	212	239	246	258	261	228	225	185	181	197	197
1951	232	279	285	305	378	388	289	269	247	251	236	247
1952	265	265	254	284	296	275	256	251	215	234	218	244
1953	245	343	308	325	328	232	286	283	249	239	199	224
1954	221	220	226	226	242	256	212	200	195	178	239	202
1955	234	232	263	254	235	241	223	174	177	152	161	178
1956	222	264	262	269	246	252	204	229	202	178	190	175
1957	240	325	355	400	393	371	319	267	233	259	281	332
1958	383	341	280	291	290	297	283	216	202	207	229	245
1959	309	317	317	286	249	270	240	240	171	211	220	207
1960	223	253	196	237	223	266	219	221	195	219	219	223
1961	272	261	285	236	280	258	245	245	193	195	181	244
1962	270	241	248	290	241	273	268	244	236	193	208	188
1963	228	251	260	264	285	294	269	247	218	230	245	243
1964	217	234	222	208	224	221	241	196	181	178	165	182
1965	214	281	373	314	273	291	329	270	282	207	300	269
1966	270	227	213	239	233	264	257	212	198	214	193	207
1967	231	233	236	240	287	248	240	195	166	177	182	205
1968	216	207	240	240	221	267	282	237	245	254	220	222
1969	262	296	337	387	306	277	274	250	285	237	300	272
1970	312	309	283	278	331	328	246	236	231	226	205	218
1971	211	270	288	302	279	226	224	219	220	234	212	215
1972	237	287	350	317	381	402	379	318	319	287	354	421
1973	316	276	212	201	227	217	229	193	198	179	186	187
1974	230	202	268	276	295	301	290	275	236	322	325	319

real-time as BATHY messages for support of real-time ocean analyses. BATHY messages, although more timely, require additional editing to correct digitizing and transmission errors. With improved digital data acquisition and satellite data transmission systems, the time lags and transmission errors are being reduced.

Subsurface temperature profiles from many available sources have been assembled by FNOC in the Master Oceanographic Observations Data Set (MOODS). MOODS is in a compact binary format and contains almost 5 million subsurface temperature profiles globally. The MOODS file is by no means a complete file of all ocean temperature profiles that have even been made; rather, it is only that subset which have been made available to FNOC and merged into the file. Probably many additional profiles exist and if obtainable, could be used to improve analyses of historical conditions. At present, MOODS occupies 12 reels of magnetic tape and is sorted in the sequence: month, 1 degree square of latitude and longitude, year, day and hour. For compactness, many of the temperature profiles are stored at significant or inflection points so that the original data can be recreated by linear interpolation between inflection points.

The distribution of the profiles in time and space is critical for making consistent time series of subsurface temperature. A total for all years of only 12,102 profiles were available in the MOODS file for the five areas along the Peru coast (Fig. 3). Temperature profiles off Peru are almost nonexistent in the MOODS file for the years prior to 1955 but are more abundant for the years from the late 1950s to the early 1970s. Lags in data assimilation have reduced the amount of data in MOODS since the mid-to-late 1970s, with most of the recent data being acquired via BATHY messages. Profiles taken prior to 1952 have been included in the analysis by combination into the single composite year, labelled "1951" in the plots and tables. Inclusion of early profiles in the analysis is useful to help establish the edition scheme and to improve the long-term means.

In addition to an insufficient quantity of profiles over the 33-year analysis period, many of the available profiles are very "patchy" in their distribution. A cell in the data fields having 100 or more observations is often surrounded by many cells with no observations. This inhomogeneity of the data fields reflects the fact that relatively large numbers of temperature profiles are taken during short, localized research expeditions.

The subsurface temperature profiles in the MOODS file suffer from many types of errors. Teague et al. (1985) have described some of the errors based on samples of the data for the North Atlantic. Many of the profiles have erroneous spikes and tails which require editing, whereby the profiles are truncated to retain the portion of the profile above the erroneous data. About 1 to 5% of the profiles are from incorrect positions or times, as evidenced by reports from land areas. No attempt was made in this analysis to correct for position and time errors of the profiles as this would have required resorting the profiles into original cruise sequences and tracking each ship individually.

Because of the errors in profiles and more importantly insufficient distribution of observations in time and space, a complicated scheme was necessary to compute reasonable monthly mean values. Thus, the MOODS profiles were edited, monthly means were computed, and then the means were interpolated to fill gaps in coverage.

Editing Scheme for Subsurface Temperature Profiles

The first stage of editing the profiles was a gross error check requiring all reported temperatures to be in the range of -2.0 to +38.0°C and all depths to be nonnegative and increase sequentially. No two temperatures were allowed from the same reported depth; in such cases (which are rare), the depth of the second reported temperature was increased by an arbitrary value of 1 m. In order to eliminate gross error spikes, the size of allowable temperature changes between successive reported depth levels was limited between +2.0 and -12.0°C. When data were rejected by these edits, the profile was truncated at the depth of failure and the remaining upper portion of the profile was retained.

The second stage of profile editing checked for unusually strong positive and negative vertical temperature gradients to further reduce unreal spikes and vertical gradients. In the surface layer and thermocline, where the water temperatures were greater than 6.0°C, the vertical temperature gradients were required to be in the range of -2.0 to +0.5°C per meter of depth. For reported temperatures less than 6.0°C, the allowable gradients were tightened to -0.5 to +0.1°C/m. As for the first stage editing, when gradients exceeding these limits were encountered, the profiles were truncated and the remaining, upper portions of the profiles were retained.

The third stage of editing was a check against the mean and standard deviations of a running series of 10 values of a temperature editing parameter. For SST, depths of the 14°C and SST-2°C isotherms and heat content, the computed parameter itself was used as the editing parameter. For the vertical temperature series, the temperature at 100 m was interpolated from each profile and used as the editing parameter. The running series was started with the first 10 profiles for each month and 1 degree square of latitude and longitude. (Because the data were sorted in the sequence: month, 1 degree square, year, day and hour, the first 10 profiles in a one degree square were often from years earlier than 1952 and thus errors in the first 10 profiles did not cause serious contamination of the 1952-1984 time series). After acceptance of the first 10 profiles, the mean and standard deviation of the running series of 10 editing values were computed and used to check the next profile. A new profile was accepted if the editing parameter computed from it was within a specified tolerance of the mean of the previous 10 values, where the tolerance was arbitrarily defined to be 1.3 times the standard deviation of the previous 10 values. Each new accepted value was then added to the series and the oldest value in the series deleted. Use of the running series of 10 values allowed the editing mean to move up or down with warm and cold periods defined by the data themselves. Similarly, the scheme allowed the editing tolerance range to widen as the data became more variable (in periods of climatic change or in areas near oceanic boundaries) and to narrow as the data became less variable (during more stable periods or in areas far from oceanic boundaries).

Computation of Individual Monthly Mean Values

After editing the temperature profiles as described above, values of the four parameters (SST, depth of the 14°C isotherm, depth of the SST-2°C isotherm, and heat content down to the SST-2°C isotherm were computed for each profile. Individual monthly means of the four parameters were computed for each cell (5 areas x 408 months) for the years 1951 to 1984. The resulting monthly mean fields were very sparse, having mean values in only about 37% of the 2,040 total cells.

Temperatures at 25 m depth intervals from the surface to 350 m were computed from each profile to display vertical variations of temperature versus time in each of the five areas. The data were processed as differences between the surface temperature and the temperature at each 25 m depth interval because of the effect of varying maximum depths of the profiles. Direct computation of mean temperatures from profiles of varying maximum depth can cause unrealistic subsurface temperature gradients (Robinson and Bauer 1976).

After computation of the individual monthly mean values, the 12 long-term monthly means and 12 between-year standard deviations were computed for each area (or depth for the vertical plots). Here, long-term mean is defined as the mean of all the individual monthly means, e.g., the January long-term mean is the mean of all individual January monthly means. The between-year standard deviation (bysd) is the standard deviation of the individual monthly means computed by month to show the interannual variability. The monthly anomalies were then computed as the differences between the individual monthly means and the appropriate long-term monthly mean, e.g., the January 1952 anomaly is the individual monthly mean for January 1952 minus the January long-term mean.

In some cases, no profiles were available in a month during any year for an area (or depth). In these cases, it was not possible to compute a long-term monthly mean. Such gaps in the long-term mean field were filled using a 5 x 5 matrix interpolation which used information from surrounding long-term means. Empty cells were filled with averages of surrounding mean values, weighing proportionately to the square root of the number of years of data represented by the mean and inversely to the square of the distance (in grid lengths) away from the cell.

The fields of individual monthly mean values were rather noisy, particularly those computed from small numbers of profiles which are considered less reliable than those based on relatively large numbers of profiles. To reduce the errors associated with limited numbers of profiles, the individual monthly means were adjusted toward the long-term mean for each month, i.e., means based on only a single profile were set to the average of the mean and the long-term mean for that month, while means based on two or three profiles were weighed proportionately less toward the long-term mean.

Monthly anomalies were computed as the difference of the adjusted individual and long-term monthly means. To partially fill the gaps in the anomaly field between data values, the same 5 x 5 matrix interpolation scheme was used as for the long-term means, weighing proportionately with the square root of the number of profiles represented by the mean and inversely with the square of the distance away from the cell. In regions that were 3 or more cells away from mean values, no interpolation of the anomaly was made. Use of this interpolation scheme increased coverage of the field from about 37% to about 91%. Use of a 5 x 5 matrix interpolator was reasonable as autocorrelation functions (not shown) of the individual monthly means were computed and had magnitudes greater than 0.4 for lags of at least two months in time and at least three areas (9 degrees of latitude) along the coast in space. The correlations are in agreement with Enfield and Allen (1980) who showed similar strong coastwise coherence of sea level and SST along the coast of North and South America from Alaska to Chile.

After adjustment and interpolation of the anomaly field, the fields of individual monthly means were recomputed. Gaps in the coverage were partially filled by the addition of the interpolated anomaly field and the long-term mean field. Use of the anomaly fields to interpolate the monthly mean fields for filling gaps in coverage is based on the assumption that the anomaly fields are smoother in time and space than the monthly means. This assumption is justified because of the large seasonal changes that are observed in the monthly means but relatively smoother changes in the anomalies (see, e.g., Fig. 2, autocorrelation functions).

Spatially Averaged Monthly Means for the 4 to 14°S Region

Monthly anomalies for the three central areas were further averaged to make time series of monthly mean anomalies for the entire region from 4 to 14°S. The averaged monthly anomalies were then added to the appropriate averaged long-term means to obtain time series for the four computed parameters by month for the region 4-14°S. Plots and tables of the time series values are presented along with the total combined number of observations for the three central areas. Values are only given if observed or interpolated mean values were available for all three areas. This requirement reduced the coverage of the time series to about 90% of the 408 possible months. For cases where anomaly values were not available for each of the three areas for any particular month, asterisks are printed in the tables and values are not plotted.

Results and Discussion

Each of the parameters (SOI, SST, sea level, depth of the 14°C isotherm, depth of the SST-2°C isotherm, vertical structure of subsurface temperature and heat content from the surface to the SST-2°C isotherm) is presented separately. The data are displayed in a variety of formats to emphasize the seasonal and interannual scales of variability, both horizontally along the coast and vertically through the water column. For each of the parameters, tables and plots of spatially-averaged (for the region from 4-14°S) monthly means are presented. Plots of the long-term annual cycle, between-year standard deviation, monthly anomaly in standard deviation units, and autocorrelation functions of the anomalies for each of the parameters are presented to describe seasonal and interannual variability. Also, time-latitude and time-depth contour plots of profile data are presented to show horizontal and vertical variations of subsurface temperature.

Southern Oscillation Index

Time series of the monthly mean Southern Oscillation Index (Fig. 1A, Table 1) and anomaly of SOI (Fig. 2A) show the buildups and subsequent declines of pressure differences associated with the onset of El Niño, as described earlier. Major buildups and declines occurred in 1949-1952, 1954-1958, 1970-1972 and 1975-1977. The most recent decline in 1982-1983, associated with that strong El Niño, followed a long period (1976-1981) of relatively weak negative pressure difference. There was also a sharp decline in 1979 associated with a weak coastal warming event in that year. Perhaps the 1979 event would have been more notable (more comparable to other moderate or weak El Niños) if it had not occurred during an already warm period.

The SOI has a relatively strong annual cycle (Figs. 1 and 2) which varies from a peak difference of about 13 mbs in February, indicating strongest trade winds in late austral summer to a low of about 7 mbs in May, indicating weakest trade winds in late austral fall. The interannual variability of SOI is relatively constant throughout the year as indicated by the similar values of between-year range and standard deviation. The SOI is moderately persistent in time with an autocorrelation of anomaly of about 0.4 at one month lag. From 12 to 36 months lag, the autocorrelation of the anomaly remains very close to zero, then becomes weakly positive at lags of 36-48 months. This suggests that the period of important interannual changes in the SOI is greater than 3 years, in agreement with the frequently reported period for El Niño of 3-7 years.

Sea Surface Temperature

Time series of monthly mean SST (Figs. 1B and 1C, Tables 2 and 3) and anomaly of SST (Figs. 2B and 2C) at Talara and La Punta (Callao) and spatially-averaged SST for the region from 4-14°S (Table 6, Figs. 4A, 5A) show significant seasonal and interannual variability of SST. Both the shore station and spatially-averaged SST data show the major El Niño and anti-El Niño events. Positive anomalies occurred in the years 1953, 1957-1958, 1965, 1972-1973, 1976-1977, 1979 and 1982-1983. Each of the figures also show longer period interannual variations: cool conditions in the early 1950s, warm conditions in the late 1950s, moderately cool conditions throughout the 1960s and early 1970s (except the 1965 and 1972-1973 El Niños), and finally a long-term warming during 1976-1983. Comparison between the two shore stations, Talara in the north and La Punta in the south, shows the northerly station to have more low-amplitude, high frequency variability than the southerly station. This difference is assumed to be caused by the more complicated equatorial ocean dynamics occurring in the northern region.

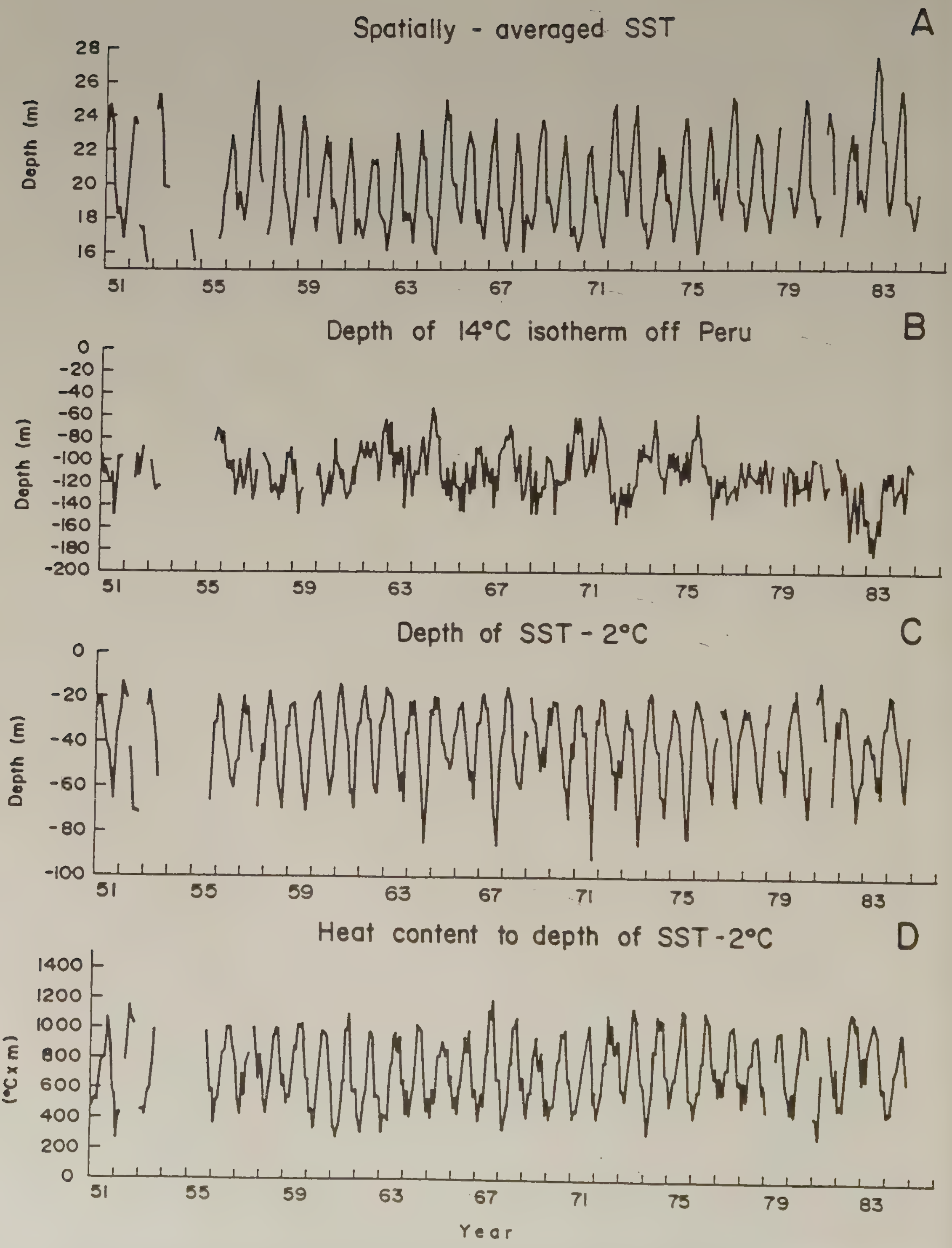
Along the coast, the El Niño events of 1953, 1957-1958, 1965, 1969, 1972-1973, 1976-1977 and 1982-1983 (Rasmusson 1984) are seen as tongues of warm SST, extending variable distances southward (Fig. 6). A moderate warming occurred in 1979-1980, in agreement with the below normal SOI that year. The extreme magnitude (large region of SST > 28°C), duration, and coastwise coherence of the 1982-1983 event distinguish it as the most significant warm feature of this series. The poorly documented 1953 El Niño shows a surprisingly strong surface manifestation of warm water. The 1954-1956 cold event is only weakly evident, probably due to sparse data. With the exception of the 1982-1983 warm event, each of the warm surface events are shown to be preceded by a period of anomalously cool SST.

The annual cycles of SST at the two shore stations (Figs. 2B and 2C) and for the spatially-averaged region (Fig. 7A) vary from highs during the austral fall to lows during the austral spring. The amplitude of the annual variation of SST is greatest nearer to the equator and the complex dynamics associated with the interaction of equatorially-trapped waves with the eastern boundary (Fig. 6). The spatially-averaged long-term means (Fig. 7A) show high SST (>23.5°C) from January through March or April, when warm water intrudes from the north, followed by a rapid transition to lower temperatures in April with the onset of upwelling along the central and southern portions of the coast. SSTs of 17-19°C occur during the upwelling regime from May to October along the coast, except for the northernmost area where upwelling is weak.

Along the coast, the annual cycle is strong, varying between upwelling and nonupwelling regimes for the central and southern areas and the weak seasonal variation for the northern area.

Table 6. Monthly mean surface temperature (C) for the region 4-14° off Peru. These means are averages of the monthly means for the three Central areas, computed from subsurface temperature profiles. The corresponding number of profiles used in computing each mean is printed (in brackets) to the right of the mean. Means based on zero profiles are computed from interpolated values. Asterisks indicate months in which neither observed nor interpolated means were available in all three areas.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1951	23.0 (1)	24.3 (1)	24.5 (129)	23.5 (0)	19.5 (0)	18.2 (2)	18.5 (36)	17.6 (6)	16.8 (0)	17.6 (0)	19.2 (0)	21.0 (0)
1952	22.8 (35)	23.9 (0)	23.6 (0)	**** (0)	17.5 (0)	17.3 (0)	17.4 (129)	16.2 (0)	15.4 (0)	**** (0)	**** (0)	**** (0)
1953	24.4 (0)	25.2 (0)	25.1 (49)	23.1 (93)	19.8 (23)	19.8 (0)	19.7 (0)	**** (0)	**** (0)	**** (0)	**** (0)	**** (0)
1954	**** (0)	**** (0)	**** (0)	**** (0)	**** (0)	**** (0)	17.3 (0)	16.3 (2)	15.5 (0)	**** (0)	**** (0)	**** (0)
1955	**** (0)	**** (0)	**** (0)	**** (0)	**** (0)	**** (0)	**** (0)	**** (0)	16.8 (0)	17.2 (0)	19.3 (51)	19.7 (95)
1956	21.0 (5)	22.5 (0)	22.8 (0)	22.0 (31)	18.5 (0)	18.4 (0)	19.5 (0)	18.5 (0)	17.8 (31)	18.3 (0)	19.9 (13)	21.5 (0)
1957	23.9 (0)	24.8 (1)	26.1 (33)	23.3 (25)	20.6 (0)	20.1 (0)	**** (0)	**** (0)	17.0 (0)	17.6 (0)	18.8 (15)	21.3 (6)
1958	23.1 (75)	24.5 (10)	24.1 (66)	22.8 (8)	19.6 (4)	19.0 (0)	18.6 (7)	17.2 (0)	16.4 (74)	17.1 (0)	18.6 (5)	21.0 (160)
1959	22.7 (0)	23.9 (0)	23.8 (32)	22.6 (0)	19.2 (0)	**** (0)	**** (0)	18.0 (0)	17.2 (0)	17.9 (4)	19.4 (0)	20.5 (0)
1960	21.4 (0)	22.8 (4)	21.6 (13)	22.3 (51)	18.5 (4)	19.0 (0)	18.7 (0)	17.3 (0)	16.5 (14)	16.8 (97)	18.1 (41)	20.1 (0)
1961	21.5 (0)	22.7 (79)	21.5 (63)	20.2 (60)	17.0 (0)	17.9 (14)	17.7 (9)	17.0 (156)	16.8 (29)	17.5 (8)	19.0 (1)	20.1 (0)
1962	21.4 (93)	21.2 (89)	21.4 (24)	20.8 (98)	18.3 (94)	18.1 (37)	17.7 (47)	16.9 (0)	16.1 (0)	16.9 (18)	17.8 (274)	20.1 (61)
1963	21.6 (33)	22.9 (178)	22.2 (55)	20.7 (69)	17.8 (0)	18.3 (0)	17.9 (55)	18.2 (142)	17.6 (46)	16.6 (155)	18.8 (44)	19.9 (72)
1964	21.7 (0)	23.1 (10)	21.5 (38)	21.5 (0)	18.5 (42)	18.0 (65)	18.0 (3)	16.4 (47)	15.9 (49)	16.0 (8)	18.6 (175)	20.6 (2)
1965	22.6 (0)	24.9 (10)	23.8 (1)	24.1 (43)	20.4 (0)	19.9 (0)	19.9 (31)	18.6 (66)	18.0 (49)	17.7 (26)	19.4 (135)	21.5 (15)
1966	22.2 (0)	23.0 (80)	22.5 (57)	22.0 (17)	18.5 (50)	17.7 (9)	18.5 (0)	17.5 (5)	16.8 (148)	16.9 (2)	18.7 (28)	20.0 (49)
1967	21.8 (0)	22.7 (116)	23.8 (15)	21.4 (5)	18.5 (45)	18.6 (2)	17.8 (2)	16.6 (95)	16.1 (69)	16.5 (0)	18.3 (28)	18.9 (48)
1968	21.3 (0)	22.9 (97)	22.2 (0)	20.8 (2)	16.1 (55)	16.0 (0)	18.1 (0)	18.0 (0)	17.6 (86)	17.4 (38)	18.1 (12)	20.3 (71)
1969	22.4 (46)	23.3 (20)	23.7 (8)	23.0 (2)	18.9 (0)	19.2 (8)	18.7 (53)	17.8 (36)	17.2 (159)	17.5 (0)	18.9 (62)	20.2 (19)
1970	21.9 (0)	22.8 (0)	21.4 (0)	20.3 (0)	17.1 (8)	17.0 (33)	17.5 (0)	16.8 (0)	16.1 (63)	16.7 (94)	17.0 (100)	18.3 (32)
1971	20.6 (0)	21.8 (0)	22.2 (0)	20.3 (5)	18.9 (23)	19.3 (19)	18.4 (0)	17.2 (151)	16.5 (43)	16.3 (11)	18.4 (109)	19.6 (62)
1972	22.4 (1)	24.3 (19)	24.7 (68)	23.3 (68)	20.8 (14)	20.5 (1)	20.7 (31)	19.5 (0)	18.2 (0)	18.2 (20)	20.6 (139)	22.1 (4)
1973	23.7 (0)	24.6 (16)	22.6 (89)	20.6 (6)	18.1 (2)	17.4 (0)	17.8 (6)	16.3 (33)	16.5 (25)	17.1 (1)	18.9 (0)	19.3 (0)
1974	22.2 (2)	20.5 (28)	21.7 (38)	21.2 (5)	19.0 (4)	19.4 (34)	18.9 (3)	17.7 (6)	16.7 (0)	17.4 (3)	18.6 (65)	20.5 (0)
1975	22.5 (6)	23.7 (2)	23.8 (53)	22.5 (29)	19.6 (37)	18.8 (1)	18.1 (0)	16.8 (133)	15.9 (0)	16.3 (0)	17.6 (13)	20.0 (17)
1976	21.6 (0)	23.3 (0)	23.3 (4)	22.0 (21)	19.1 (0)	19.8 (0)	20.3 (25)	18.3 (26)	17.9 (0)	19.2 (16)	20.2 (0)	21.6 (27)
1977	23.6 (0)	25.0 (26)	24.7 (0)	23.5 (1)	19.5 (0)	19.0 (9)	18.9 (0)	17.6 (13)	17.3 (0)	18.4 (11)	19.0 (11)	20.8 (0)
1978	22.0 (0)	22.9 (0)	22.6 (5)	22.1 (0)	19.7 (1)	18.7 (0)	18.3 (9)	17.4 (0)	17.2 (0)	18.3 (0)	19.9 (19)	21.5 (0)
1979	23.3 (0)	**** (0)	**** (0)	**** (0)	**** (0)	19.8 (0)	19.8 (0)	18.8 (28)	18.1 (0)	18.5 (0)	19.5 (0)	21.1 (8)
1980	23.4 (0)	24.9 (4)	24.7 (11)	23.7 (0)	20.0 (0)	19.3 (0)	19.3 (0)	18.4 (12)	17.6 (0)	18.2 (0)	**** (0)	**** (0)
1981	23.0 (0)	24.1 (0)	23.6 (21)	2.8 (0)	19.5 (0)	**** (0)	**** (0)	**** (0)	17.1 (0)	17.8 (0)	19.2 (34)	21.4 (19)
1982	22.4 (0)	22.8 (1)	21.5 (29)	22.4 (21)	18.9 (0)	19.6 (0)	19.6 (0)	18.6 (19)	18.5 (0)	20.5 (0)	22.6 (34)	23.4 (6)
1983	26.0 (0)	27.4 (17)	26.5 (1)	26.0 (31)	22.5 (0)	22.4 (30)	21.5 (18)	19.0 (2)	18.3 (0)	19.1 (11)	20.4 (0)	22.2 (0)
1984	24.1 (0)	25.3 (12)	25.0 (0)	23.7 (0)	19.0 (0)	19.0 (0)	18.8 (11)	18.2 (12)	17.4 (0)	17.9 (0)	19.4 (7)	**** (0)



Spatially - averaged SST

Depth of 14°C isotherm off Peru

Depth of SST - 2°C

Heat content to depth of SST - 2°C

Fig. 4. Time series of spatially-averaged monthly means for the region 4 to 14°S as computed from profiles of subsurface temperature. Parameters are (A) SST, (B) depth to 14°C isotherm, (C) depth to SST-2°C isotherm, and (D) heat content from the surface down to SST-2°C.

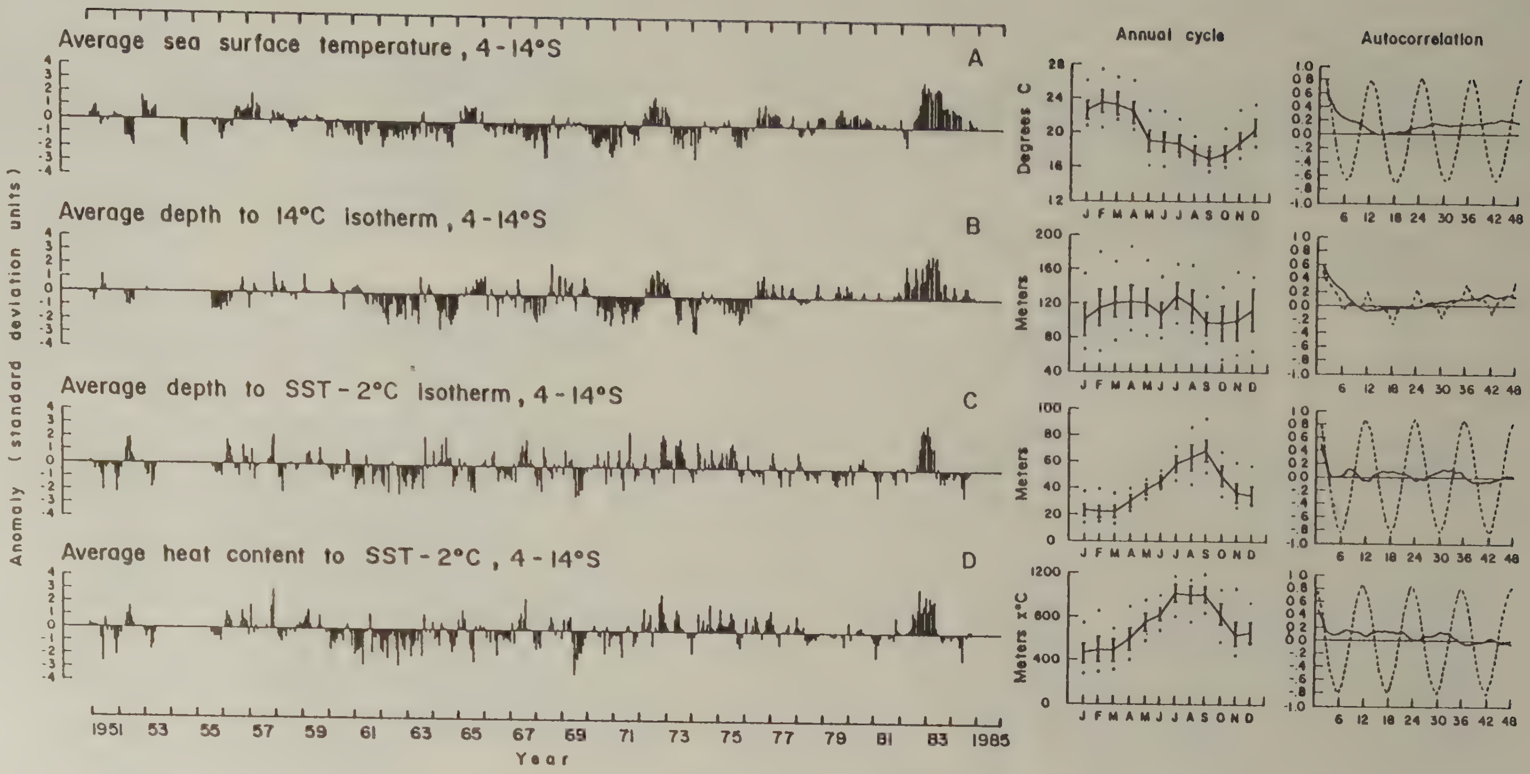


Fig. 5. Annual cycles, autocorrelation functions, and anomalies of (A) SST, (B) depth of the 14°C isotherm, (C) depth of SST-2°C isotherm, and (D) heat content from the surface down to SST-2°C isotherm off Peru from 1952 to 1984. Data shown for "1951" are a composite of data for all years prior to 1952.

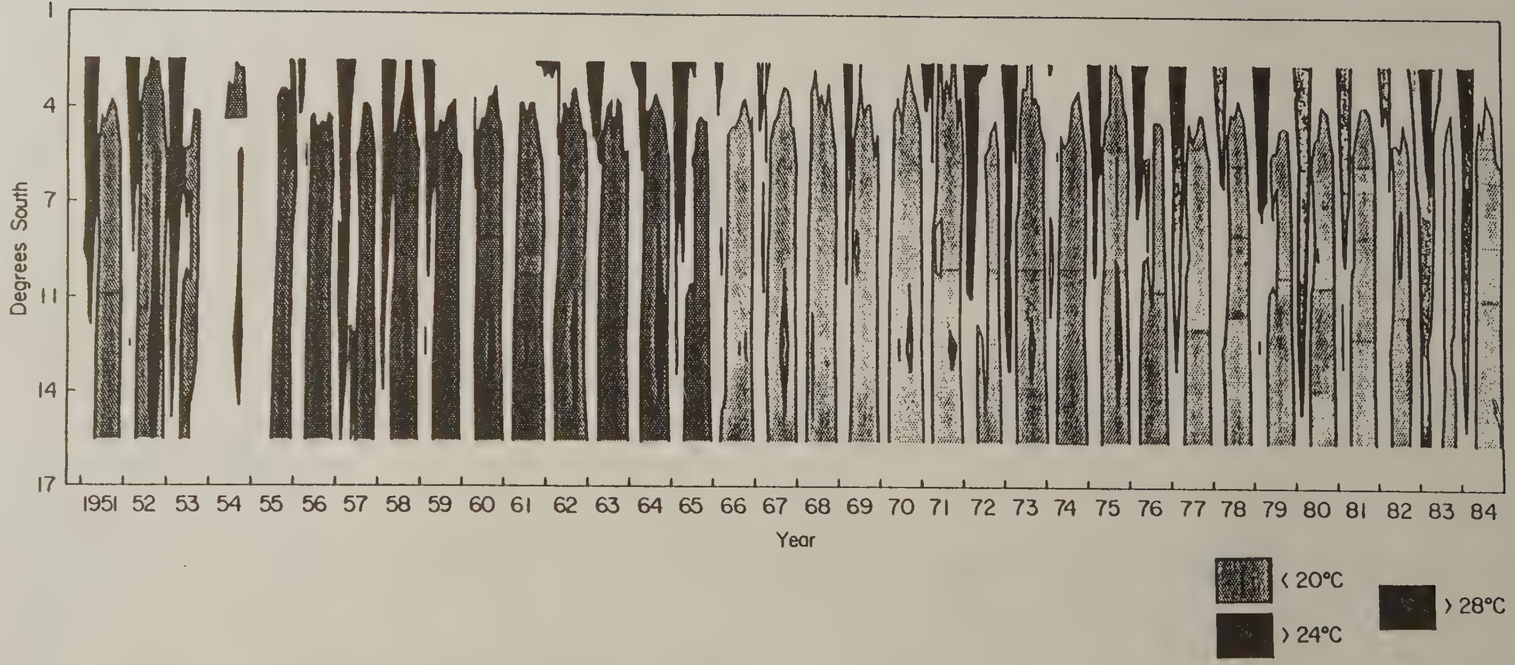


Fig. 6. Time-latitude contour plot of monthly mean SST for the 5 areas off Peru. Data shown for "1951" are a composite of data for all years prior to 1952. Tongues of water greater than 24°C penetrate a variable distance southward along the coast during January to March from year to year and are indicators of El Niño. Water of greater than 28°C intruded southward in early 1983. Low temperature tongues, associated with upwelling, extend northward.

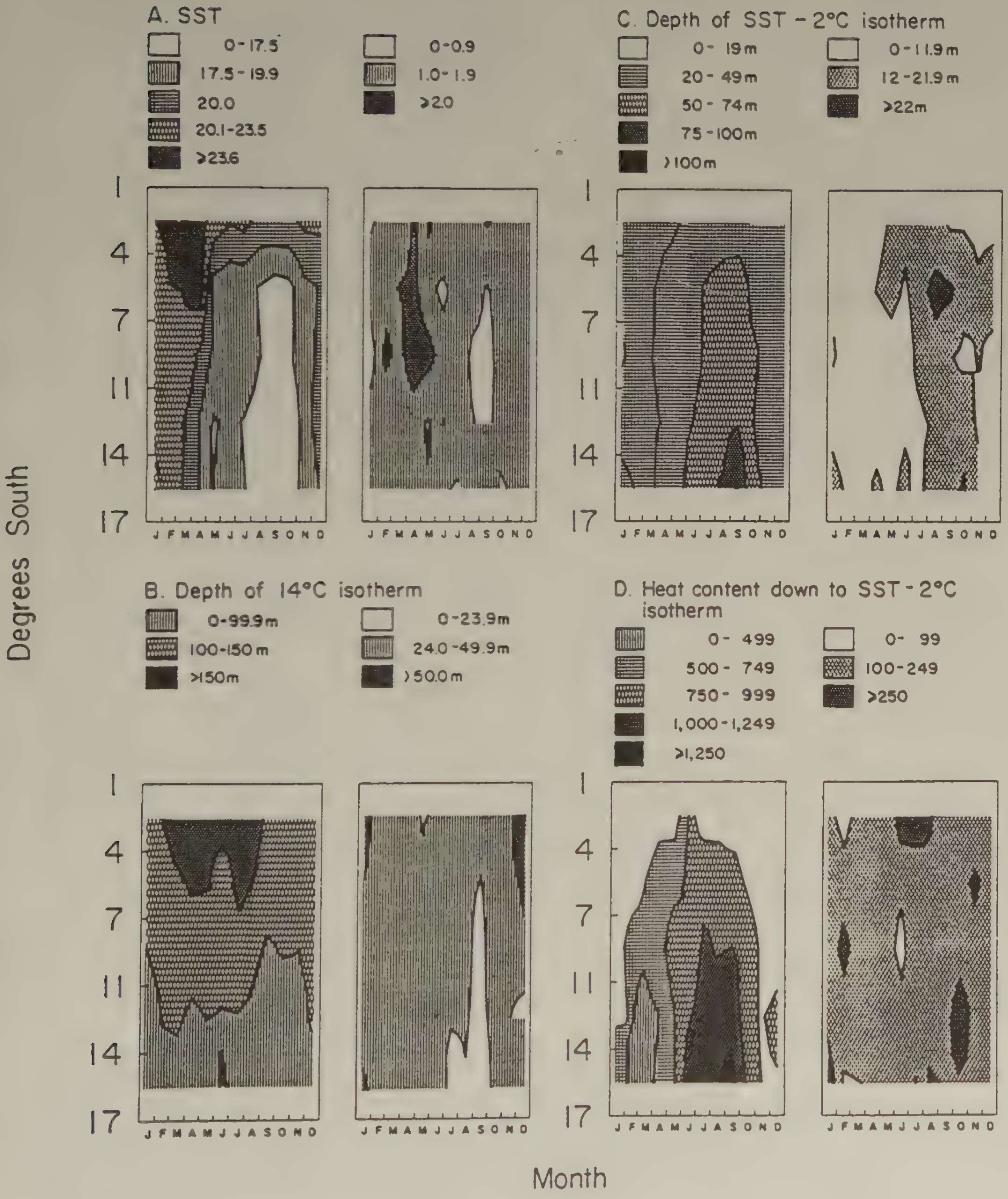


Fig. 7. Time-latitude contour plots of annual cycles and between-year standard deviations of (A) SST, (B) depth of 14°C isotherm, (C) depth of SST-2°C isotherm, and (D) heat content down to SST-2°C isotherm for 5 areas along the Peru coast. The long-term mean annual cycles are shown in the left-hand plots. When no profiles were available for a month in any year, the long-term mean was interpolated. The between-year standard deviations are shown in the right-hand boxes.

The time-latitude between-year standard deviation plot (Fig. 7A, left-hand plot) shows the highest interannual variability to occur during the fall transition from the warm current regime to the upwelling regime, particularly in area 2 which is between the strong upwelling to the south and the weak upwelling to the north. The interannual variability of SST is lowest during peak upwelling.

The autocorrelation function of the anomaly of the spatially-averaged SST (Fig. 5A) is moderately persistent with a lag one value of about 0.6. After 18 months' lag, the autocorrelation function begins to rise, peaking again at a lag of about 44 months. Anomaly of SST at the two shore stations has autocorrelation functions with moderately strong persistence at lags one and two, negative correlation between lags of 12 and 36 months, and weakly positive correlation after a lag of about 40 months (see Figs. 2B, 2C). This pattern is similar to that described for SOI.

Vertical Structure of Subsurface Temperature, 0-350 m

The interannual variability of subsurface temperature for the central area (Area III) off Peru (Fig. 8) shows monthly variations of isotherm depths from the surface to 350 m for the period 1952 to 1984. A similar plot of the anomaly field was used for the analysis (but not shown because anomalies must be carefully analyzed to avoid misinterpretation of events caused by slight phase shifts). Interestingly, the 12, 14 and 16°C isotherms show a general long-term depression of the thermal structure for the period 1976-1984, in agreement with the changes in SOI and SST discussed previously and with other reports of a large-scale coastal warming during the period.

Shorter duration depressions of the isotherms are observed for the 1957-1958, 1965-1966, 1969, 1972-1973, 1976-1977, 1979-1980 and 1982-1983 El Niño warming events. The magnitude and vertical extent of these isotherm depressions varies noticeably between different events. Each of these El Niño events is characterized by moderate to strong surface warming. The anomaly field (not shown) has double peaks for most of these warming events, as has been reported by others for many El Niño events (e.g., Cane 1983; Reinecker and Mooers 1986). The 1957-1958 El Niño appears to be of shallower extent but of longer duration than most of the other events, lasting for about 3 years. The 1965-1966 El Niño had intense surface warming (down to 150 m) which began in January 1965 and lasted until about July, followed by a second, weaker warming which peaked in about December. There was also a weak isotherm depression between 275 and 350 m. The 1969 El Niño had a weak signal from the surface down to about 300 m. The 1972-1973 El Niño was similar in vertical extent and duration to the 1965 event, except the second peak was less defined. The 1976-1977 event was moderately strong at all depths from the surface down to 350 m. The 1979-1980 event had a weak depression at all depths. During the 1982-1983 El Niño, a strong depression of 50 to 80 m was observed at all depths. For this event, it is interesting to note that the 12 and 14°C isotherms were depressed 5-6 months prior to the depressions of the surface layer isotherms. It is yet to be determined whether this relates to the idea of downward and poleward propagating coastally trapped waves (McCreary 1976).

The annual cycles of subsurface temperatures for the five areas along the coast are shown by vertical contour plots of the long-term monthly means (Fig. 9). The areas are arranged from north to south from left to right across the page. The strongest vertical temperature gradients are in the upper 75 m, indicating a relatively shallow mean thermocline. The isotherms display a relatively linear slope upwards with increasing latitude (southward) along the coast, as would be expected. The 12 and 14°C isotherms shoal from mean depths of about 285 m and 170 m for Area I, near the equator, to mean depths of 205 m and 90 m for Area V, in the south. Similarly, the SST varies between 21 and 24°C for the northern area and between 16 to 21°C for the southern area. Each of these plots show a strong annual cycle having relatively warm temperatures during the austral summer, with annual highs occurring in February and March, and cooler temperature during the austral winter, with annual lows occurring in September. This pattern of the annual cycle becomes less apparent with increasing depth, where the 12, 14 and 16°C isotherms have an interesting double peak.

The interannual variability of subsurface temperature off Peru is shown by vertical contour plots of the between-year standard deviation (bysd, see Fig. 10) for the long-term monthly means

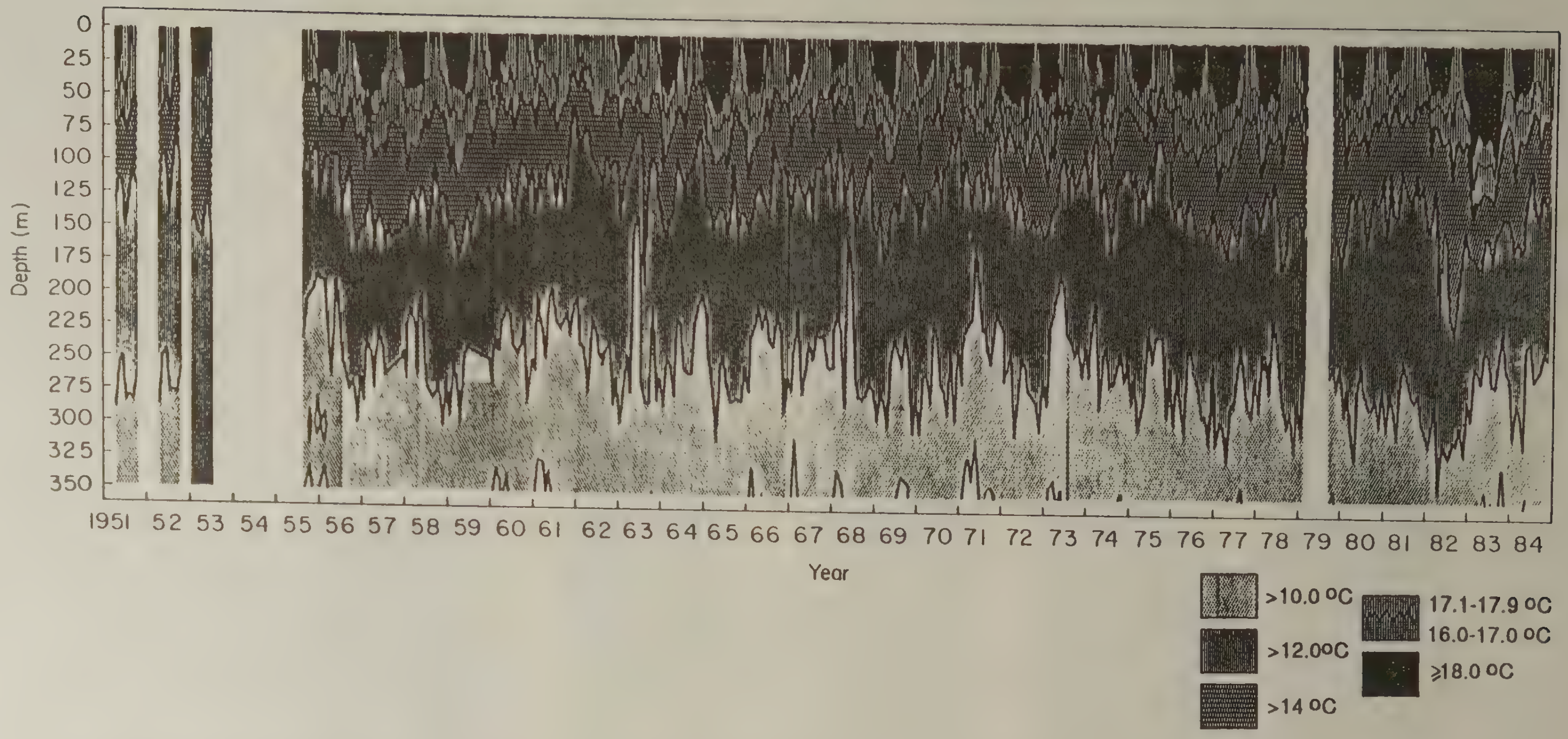


Fig. 8. Time-depth contour plot of monthly mean subsurface temperature off Peru from 1952 to 1984. Data are computed at 25 m depth intervals from 0 to 350 m from subsurface temperature profiles for central area (Area III). Values shown for "1951" are a composite of data for all years prior to 1952. Note the depression of the 12°C and 14°C isotherms from the early to mid-1970s to a maximum depth in 1982.

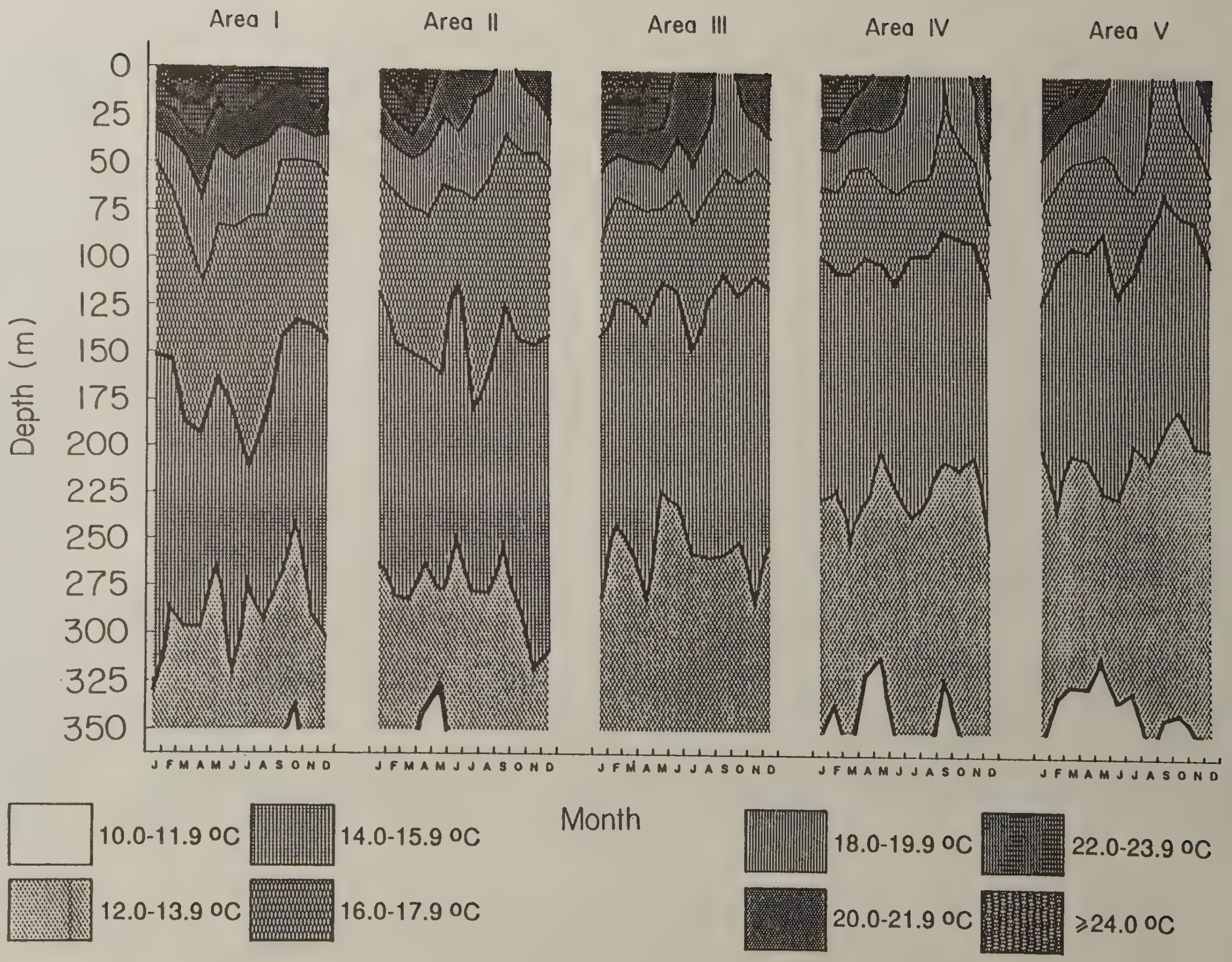


Fig. 9. Annual cycles of subsurface temperature vertically from 0 to 350 m for 5 areas along the Peru coast. Note the progressive rise of the isotherms from north (Area I on the left) to south (Area V on the right). For example, the 14°C isotherm rises from depths of 250-325 m in the north to depths of 75-125 m in the south.

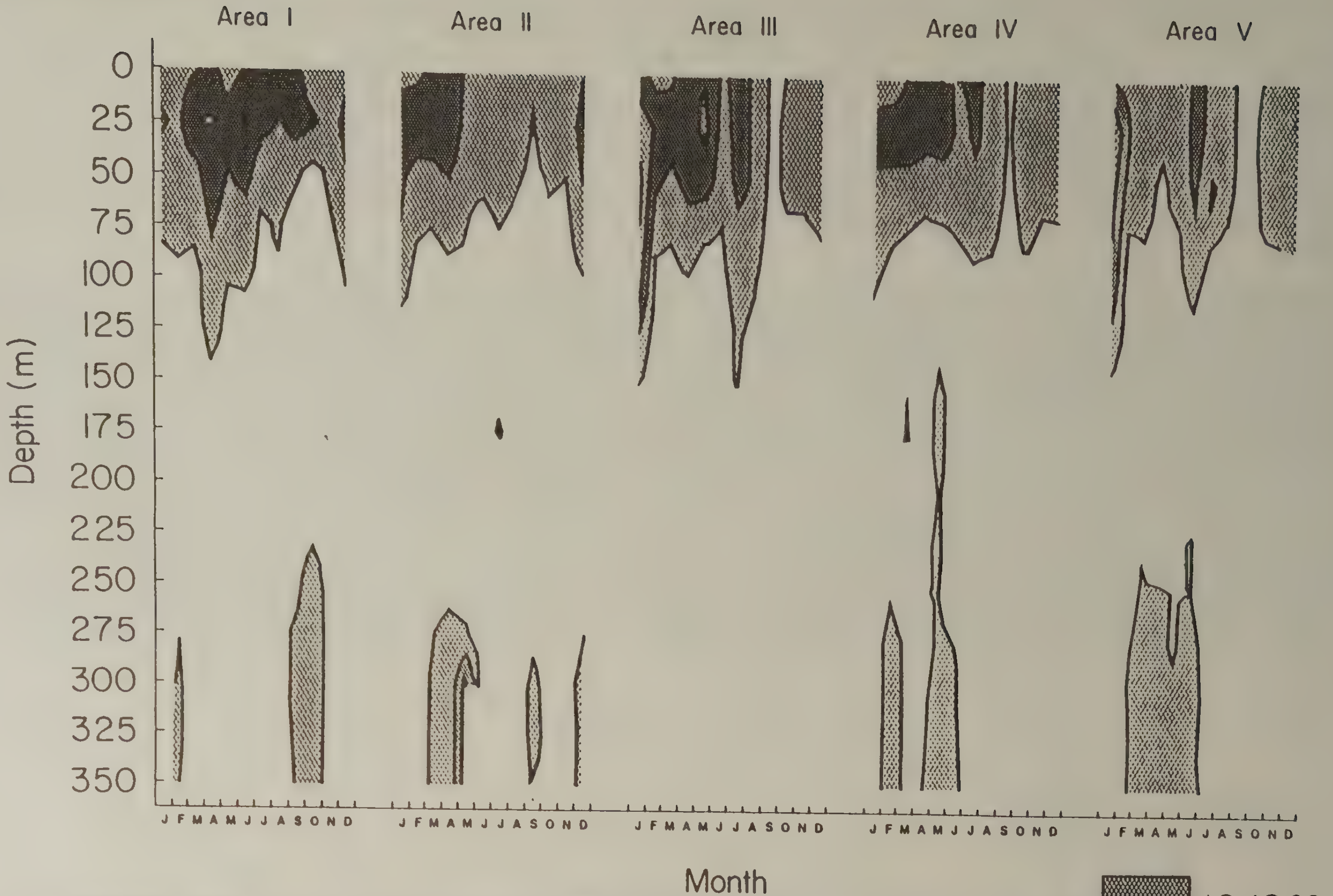


Fig. 10. Between-year standard deviation of subsurface temperature vertically from 0 to 350 m for the 5 areas along the Peru coast. The highest interannual variability occurs in the upper 100 m during the relaxed upwelling period (December to June).

just discussed. The highest variability is found in the upper 50 m, as would be expected for the thermocline. Seasonally, this upper layer variability appears to be highest (bysd = 2.7-3.0°C) from March through July and lowest (bysd = 0.7-1.2°C) in September. With a few exceptions, the interannual variability is consistently low (bysd = 0.2-0.9°C) below 100 m in each of the 5 areas.

Depth of the 14°C Isotherm

Unlike the previous section which described time variations of the thermal structure vertically for a single area and the long-term annual cycle of the slope of the thermal structure for the five areas along the coast, this section examines temporal and spatial variations of the depth of the 14°C isotherm in greater detail. The time series of monthly mean depth of the 14°C isotherm (Fig. 11, Table 7) shows considerable seasonal and interannual variability. The 14°C isotherm deepened during each of the warming events, with the most striking example occurring during the 1982-1983 El Niño. The anomaly of the depth of the 14°C isotherm (Fig. 5B) shows persistent deep or shallow anomalies lasting several years. The 14°C isotherm deepened in 1976 and remained anomalously deep throughout the rest of the record.

The annual cycle of the depth of the 14°C isotherm (Fig. 7B) differs from the annual cycles of each of the other parameters in that it displays a double peak. Seasonally, the depth of the 14°C isotherm for the region from 4 to 14°S has maximum depths in April and July and minimum depths in June and September. This double peak exists for each of the five areas (Fig. 9), although the months of occurrence differ slightly.

The 14°C isotherm is relatively deep in the north and shallow in the south (Figs. 9 and 11). The annual long-term mean depths of the 14°C isotherm for Areas I through V are 152, 135, 109, 90, and 78 m, respectively. The transition from depth to shallow depths is usually rapid, typically occurring in 1-2 months. The interannual variability of the depth of the 14°C isotherm is highest in December and January for the three northern areas (between-year standard deviations greater than 50 m), associated with the intrusion of the warm water. The interannual variability is lowest during peak upwelling in September.

Along the coast, the depth of the 14°C isotherm (Fig. 11) provides an indication of the coastwise interannual variability of the thermocline depth and the effect of coastal upwelling on the thermal structure. The 14°C isotherm deepened moderately during the years 1957-1958, 1965, 1969, 1976-1977 and 1979-1980 and strongly during the 1972-1973 and 1982-1983 El Niños. This plot shows the 1982-1983 El Niño to be the largest event of the record, both in magnitude and duration. The 14°C isotherm remained below 200 m for most of the period from February 1982 through July 1983 for the northern two areas. Likewise, the 14°C isotherm remained significantly deeper than normal during this period for the southern three areas. Both plots show the 1957-1958, 1965, 1969, 1972-1973 and 1976-1977 El Niños were preceded by cold period having shallow depths of the 14°C isotherm. The 1979-1980 and 1982-1983 warm events, by contrast, occurred during the long-term coastal warming from 1976 to 1984.

The 1979-1980 warming, which was not included in Rasmusson's (1984) list of El Niños, had moderate signals for each of the three parameters thus far discussed. Norton et al. (1984) described a strong surface warming in 1979-80 in the California current system which attenuated rapidly with depth, seemingly unrelated to tropical warming.

Wyrtki (1975) pointed out that El Niño conditions off the coast of Peru were not caused by a local weakening of the upwelling favorable winds, as had been previously hypothesized. He showed that not only did the upwelling favorable winds not weaken but also appeared to have strengthened during El Niño events. Using Bakun's (this vol.) time series of wind stress, turbulent mixing index, and offshore Ekman velocity and transport, we now strengthen Wyrtki's argument and show that each of the major El Niño events of the past three decades occurred during periods of anomalously strong southeast trades and offshore Ekman transport. One would expect intense offshore transport to be associated with intense coastal upwelling and shallow thermocline. However, comparison of the time series of offshore transport with depth of the 14°C isotherm indicates the opposite. Periods of strongest offshore transport correspond to periods of deepest depth of the 14°C isotherm. The 1957-1958, 1965, 1972-1973 and 1982-1983

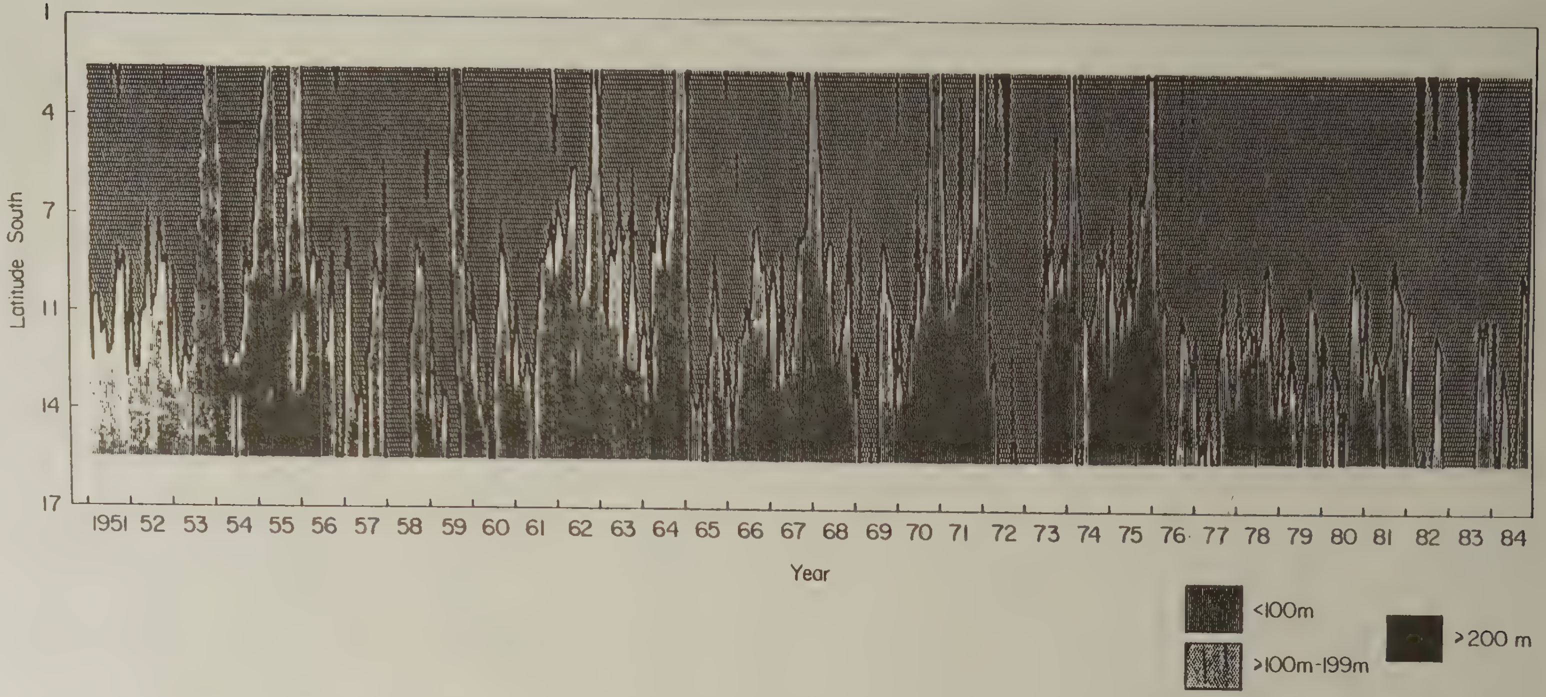


Fig. 11. Time-latitude contour plot of monthly mean depth of the 14°C isotherm for 5 areas along the coast off Peru. Data shown for "1951" are a composite of data for all years prior to 1952. The 14°C isotherm is generally shallower than 100 m in the south and deeper than 100 m in the north. The isotherm was occasionally deeper than 200 m in the northernmost areas (e.g., 1967, 1972, 1982 and 1983). Note the large region in the north during 1976-1984 when the 14°C isotherm was consistently deeper than 100 m.

Table 7. Monthly mean depth of the 14°C isotherm (m) for the region 4-14°S off Peru. These means are averages of the monthly means for the three central areas, computed from subsurface temperature profiles. The corresponding number of profiles used in computing each mean is printed (in brackets) to the right of the mean. Means based on zero profiles are computed from interpolated values. Asterisks indicate months in which neither observed nor interpolated means were available in all three areas.

Year	Jan		Feb		Mar		Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec	
1951	96	(1)	112	(1)	108	(2)	116	(0)	121	(0)	110	(0)	149	(17)	126	(7)	96	(0)	96	(0)	****	(0)	****	(0)
1952	****	(0)	****	(0)	****	(0)	****	(0)	116	(0)	94	(0)	113	(144)	106	(0)	87	(0)	****	(0)	****	(0)	****	(0)
1953	101	(0)	115	(0)	127	(1)	123	(0)	123	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)
1954	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)
1955	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	81	(0)	73	(0)	73	(69)	85	(104)
1956	75	(5)	97	(0)	108	(0)	102	(47)	110	(0)	100	(0)	131	(0)	121	(0)	99	(30)	108	(0)	126	(5)	119	(0)
1957	98	(0)	90	(3)	118	(43)	135	(10)	127	(0)	108	(0)	****	(0)	****	(0)	94	(0)	98	(0)	102	(5)	105	(2)
1958	129	(41)	128	(9)	121	(65)	127	(6)	136	(2)	113	(0)	129	(1)	118	(0)	94	(51)	96	(0)	89	(5)	112	(173)
1959	101	(0)	120	(0)	148	(5)	129	(0)	125	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	****	(0)	113	(0)
1960	103	(0)	118	(3)	140	(32)	137	(75)	128	(3)	111	(0)	130	(0)	116	(0)	81	(7)	102	(94)	105	(33)	117	(0)
1961	109	(0)	126	(55)	134	(60)	131	(15)	127	(0)	105	(12)	121	(14)	104	(124)	96	(24)	82	(8)	91	(0)	98	(0)
1962	85	(63)	96	(77)	97	(24)	88	(90)	86	(101)	96	(20)	118	(35)	110	(0)	75	(0)	68	(20)	67	(284)	95	(54)
1963	66	(88)	113	(99)	115	(40)	93	(30)	104	(0)	90	(0)	96	(60)	143	(49)	101	(3)	86	(61)	110	(14)	132	(18)
1964	109	(0)	112	(11)	113	(13)	101	(0)	81	(51)	89	(99)	113	(2)	86	(59)	73	(61)	54	(9)	60	(180)	79	(0)
1965	80	(0)	114	(0)	125	(0)	119	(34)	132	(1)	109	(0)	136	(26)	130	(53)	103	(34)	123	(21)	124	(85)	145	(18)
1966	121	(0)	145	(47)	103	(42)	122	(32)	130	(44)	106	(21)	125	(0)	89	(5)	94	(135)	87	(2)	100	(29)	123	(41)
1967	99	(0)	109	(130)	120	(11)	107	(5)	142	(52)	114	(9)	126	(2)	95	(113)	90	(63)	88	(1)	79	(31)	81	(55)
1968	70	(0)	75	(114)	96	(1)	119	(7)	102	(32)	96	(0)	134	(0)	134	(0)	128	(57)	107	(32)	88	(9)	148	(37)
1969	130	(12)	109	(15)	148	(7)	130	(2)	134	(2)	123	(14)	125	(48)	97	(31)	101	(117)	102	(0)	113	(23)	148	(8)
1970	117	(0)	121	(0)	122	(0)	119	(0)	120	(1)	87	(26)	118	(0)	101	(0)	74	(67)	62	(95)	76	(125)	63	(47)
1971	71	(0)	100	(0)	114	(0)	109	(4)	101	(22)	79	(15)	111	(0)	98	(170)	90	(47)	60	(11)	69	(112)	74	(60)
1972	81	(1)	102	(20)	113	(49)	138	(59)	130	(17)	128	(0)	157	(25)	147	(15)	124	(0)	139	(22)	130	(87)	150	(2)
1973	121	(0)	141	(11)	134	(77)	124	(14)	121	(3)	90	(0)	100	(9)	86	(36)	95	(24)	94	(0)	99	(0)	101	(0)
1974	80	(2)	64	(24)	75	(40)	107	(7)	115	(7)	115	(15)	129	(5)	112	(5)	94	(0)	105	(3)	93	(57)	109	(0)
1975	95	(8)	105	(2)	121	(53)	102	(35)	116	(63)	92	(1)	118	(0)	99	(134)	81	(0)	80	(0)	59	(17)	76	(16)
1976	81	(0)	104	(0)	104	(6)	111	(11)	121	(0)	113	(0)	151	(21)	132	(14)	115	(0)	133	(23)	120	(0)	123	(12)
1977	113	(0)	139	(24)	133	(0)	128	(0)	127	(0)	123	(2)	135	(0)	120	(14)	101	(0)	114	(11)	122	(8)	121	(0)
1978	102	(0)	113	(1)	116	(5)	119	(0)	119	(2)	105	(0)	128	(1)	117	(0)	99	(0)	111	(0)	128	(20)	124	(0)
1979	106	(0)	***	(0)	***	(0)	***	(0)	***	(0)	110	(0)	139	(0)	138	(25)	105	(0)	108	(0)	110	(0)	139	(3)
1980	113	(0)	129	(4)	125	(14)	125	(0)	124	(0)	108	(0)	135	(0)	128	(11)	99	(0)	101	(0)	***	(0)	***	(0)
1981	102	(0)	119	(0)	133	(19)	126	(0)	124	(0)	***	(0)	***	(0)	***	(0)	97	(0)	105	(0)	109	(33)	129	(17)
1982	110	(0)	118	(5)	149	(29)	171	(19)	146	(0)	121	(0)	149	(0)	164	(14)	119	(0)	125	(0)	156	(12)	151	(1)
1983	154	(10)	180	(16)	168	(6)	185	(85)	169	(7)	151	(73)	166	(68)	134	(9)	114	(0)	125	(13)	110	(0)	120	(0)
1984	111	(0)	138	(18)	132	(0)	126	(0)	125	(0)	114	(0)	145	(14)	136	(10)	103	(0)	104	(0)	109	(7)	****	(0)

El Niño periods of anomalously deep thermocline occurred during the four highest peaks of offshore Ekman transport. Thus, the thermocline deepens sharply during periods when local wind forcing should produce anomalously shallow thermocline.

Depth of the SST-2°C Isotherm

The depth of the SST-2°C isotherm is an indicator of the thickness of the surface mixed layer, i.e., the depth to the top of the thermocline. The time series of monthly mean depth of the SST-2°C isotherm (Fig. 4C, Table 8) show that variations in the depth of this isotherm occur over both seasonal and interannual time scales. Although anomalies (Fig. 5C) occurred during the major El Niño events, the interannual variations of the depth of the SST-2°C isotherm are less closely correlated with El Niño events than were the other parameters discussed. Rather, the dominant interannual variations appear to occur over longer time scales. The SST-2°C isotherm was anomalously shallow throughout most of the 1960s, anomalously deep from 1970 to 1976, near the long-term mean annual cycle from 1976 until 1982 and deep during the 1982-1983 El Niño.

The annual cycle of the depth of the SST-2°C isotherm (Fig. 7C) is strong, varying from a minimum depth of 20-25 m from January through March (austral summer) to a maximum depth of 60-70 m from July through September (austral winter). This annual cycle corresponds well with Bakun's (this vol.) seasonal wind mixing index and surface wind stress calculations, further establishing the depth of the SST-2°C isotherm as a reasonable measure of the mixed layer depth. Thus, the annual cycle of the depth of the SST-2°C isotherm fluctuates with the upwelling cycle, being deep during the upwelling season and shallow during the nonupwelling season. Upwelling elevates the thermal structure in response to offshore transport of the surface water. The elevated thermal structure combined with increased turbulent mixing during the upwelling season apparently force the observed deepening of the SST-2°C isotherm.

The between-year standard deviation and range between extrema vary between lows of about 5 and 20 m, respectively, in May and June to highs of about 20 and 40 m, respectively, in August and September (Fig. 7C). There is an inverse correlation between SST and depth of the SST-2°C isotherm. The autocorrelation function of the depth of the SST-2°C isotherm indicates weak persistence (Fig. 5C). This suggests that the mixed layer changes due to local rather than large-scale processes, which makes sense because it is primarily an indicator of the thickness of the wind forced mixed layer (or local upper layer stratification due to heat budget considerations).

Along the coast, the depth of the SST-2°C isotherm slopes from a shallow annual mean depth in the north (Area I) of 31 m to a relatively deep annual mean depth in the south (Area V) of 50 m. The maximum coastwise between-year standard deviation occurs in August in Area II, which is located between the weak upwelling area to the north and the strong upwelling areas to the south, reflecting interannual variations in the northerly extent of the upwelling.

Heat Content from the Surface to the SST-2°C Isotherm

The heat content from the surface down to the SST-2°C isotherm (Fig. 4D) is computed as the vertically averaged mean temperature down to the SST-2°C isotherm multiplied by that depth. Since the magnitudes of depth variations (in meters) are significantly greater than for temperature variations (in degrees Celsius), the computed heat contents are dominated more by depth than temperature. Thus, heat content is low (300 to 500°C x m) during nonupwelling periods when the surface layer is warm but the SST-2°C isotherm is very shallow. Conversely, heat content is high(>1,000°C x m) during the upwelling regime when the surface layer is cool but the SST-2°C isotherm is deep. Time series of monthly mean heat content (Fig. 4D, Table 9) and anomaly of heat content (Fig. 5D) reveal interannual variations almost identical to those described for the depth to the SST-2°C isotherm.

The annual cycle of heat content has characteristics similar to the annual cycle described for depth to the SST-2°C isotherm (Fig. 7D). The long-term mean values vary from about 500 mC

Table 8. Monthly mean depth of the SST-2°C isotherm (m) for the region 4-14°S off Peru. These means are averages of the monthly means for the three central areas, computed from subsurface temperature profiles. The corresponding number of profiles used in computing each mean (in brackets) is printed to the right of the mean. Means based on zero profiles are computed from interpolated values. Asterisks indicate months in which neither observed nor interpolated means were available in all three areas.

Year	Jan		Feb		Mar		Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec	
1951	24	(1)	22	(1)	20	(195)	29	(0)	37	(0)	42	(0)	45	(34)	59	(6)	66	(0)	49	(0)	35	(0)	29	(0)
1952	13	(37)	17	(0)	20	(0)	**	(0)	43	(0)	53	(0)	71	(143)	71	(0)	72	(0)	**	(0)	**	(0)	**	(0)
1953	24	(0)	20	(0)	18	(62)	26	(145)	32	(24)	40	(0)	56	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)
1954	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)
1955	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	**	(0)	66	(0)	45	(0)	32	(70)	31	(114)
1956	19	(5)	23	(0)	26	(0)	39	(47)	44	(0)	48	(0)	56	(0)	60	(0)	61	(31)	50	(0)	48	(15)	39	(0)
1957	26	(0)	20	(3)	28	(50)	25	(33)	38	(0)	45	(0)	**	(0)	**	(0)	69	(0)	53	(0)	42	(16)	48	(10)
1958	34	(78)	22	(16)	18	(90)	26	(8)	31	(4)	44	(0)	58	(4)	65	(0)	70	(54)	50	(0)	34	(5)	33	(174)
1959	24	(0)	23	(0)	23	(36)	34	(3)	43	(1)	47	(0)	58	(0)	64	(0)	71	(0)	60	(4)	40	(0)	36	(0)
1960	23	(0)	21	(7)	18	(47)	25	(107)	36	(4)	43	(0)	56	(0)	63	(0)	64	(10)	59	(92)	45	(49)	36	(0)
1961	19	(0)	14	(113)	16	(97)	25	(55)	35	(0)	40	(14)	63	(10)	62	(137)	70	(27)	39	(6)	32	(1)	32	(0)
1962	21	(102)	16	(130)	15	(35)	29	(100)	31	(107)	46	(36)	60	(27)	63	(0)	62	(0)	33	(20)	31	(273)	27	(58)
1963	16	(94)	19	(184)	19	(55)	22	(73)	34	(0)	42	(0)	54	(61)	62	(118)	54	(29)	67	(76)	36	(44)	36	(61)
1964	23	(0)	28	(13)	22	(47)	32	(0)	41	(54)	52	(95)	61	(3)	85	(37)	74	(40)	55	(7)	26	(182)	28	(2)
1965	20	(0)	25	(10)	21	(1)	32	(87)	40	(1)	41	(0)	47	(35)	48	(69)	52	(43)	50	(24)	37	(139)	35	(29)
1966	25	(0)	25	(96)	22	(65)	30	(34)	42	(69)	50	(25)	57	(0)	53	(4)	65	(130)	47	(0)	31	(29)	31	(50)
1967	20	(0)	18	(147)	24	(16)	25	(11)	41	(65)	50	(9)	69	(2)	76	(103)	86	(54)	52	(1)	42	(32)	37	(62)
1968	20	(0)	16	(120)	18	(1)	22	(7)	45	(41)	49	(0)	57	(0)	60	(0)	61	(73)	52	(36)	35	(11)	37	(73)
1969	**	(17)	20	(23)	29	(8)	31	(2)	41	(3)	48	(20)	53	(58)	42	(34)	51	(149)	37	(0)	25	(59)	32	(19)
1970	22	(0)	23	(0)	22	(0)	32	(0)	40	(3)	50	(25)	60	(0)	65	(0)	74	(55)	41	(91)	47	(129)	31	(50)
1971	24	(0)	23	(0)	25	(0)	37	(12)	36	(28)	39	(23)	62	(0)	70	(172)	92	(46)	54	(8)	30	(118)	32	(58)
1972	21	(1)	22	(26)	25	(96)	36	(90)	40	(35)	45	(2)	54	(53)	53	(17)	70	(0)	48	(31)	53	(148)	53	(21)
1973	34	(6)	26	(15)	26	(114)	34	(25)	35	(3)	53	(0)	70	(11)	86	(38)	80	(25)	57	(0)	39	(0)	34	(0)
1974	21	(2)	18	(37)	21	(45)	40	(12)	44	(7)	45	(31)	64	(5)	65	(5)	73	(0)	62	(3)	43	(68)	38	(0)
1975	26	(8)	26	(2)	29	(56)	32	(45)	44	(64)	49	(1)	70	(0)	83	(141)	82	(0)	56	(0)	34	(15)	29	(19)
1976	22	(0)	23	(0)	28	(6)	30	(17)	38	(0)	44	(0)	57	(42)	59	(27)	67	(0)	42	(26)	38	(0)	**	(17)
1977	26	(0)	29	(27)	25	(0)	31	(0)	37	(0)	41	(11)	59	(0)	66	(14)	68	(0)	41	(13)	36	(9)	34	(0)
1978	25	(0)	29	(1)	26	(5)	32	(0)	38	(2)	43	(0)	54	(4)	61	(0)	66	(0)	46	(0)	31	(21)	33	(0)
1979	23	(0)	**	(0)	**	(0)	**	(0)	**	(0)	43	(0)	52	(0)	52	(29)	63	(0)	47	(0)	35	(0)	28	(8)
1980	22	(0)	25	(4)	18	(17)	29	(0)	39	(0)	48	(0)	62	(0)	73	(13)	72	(0)	51	(0)	**	(0)	**	(0)
1981	22	(0)	19	(0)	13	(21)	27	(0)	38	(0)	**	(0)	**	(0)	**	(0)	67	(0)	46	(0)	30	(36)	37	(19)
1982	24	(0)	24	(5)	24	(36)	27	(24)	39	(0)	45	(0)	58	(0)	63	(23)	74	(0)	64	(0)	59	(81)	57	(21)
1983	37	(14)	39	(32)	36	(6)	39	(99)	46	(7)	44	(99)	60	(80)	55	(11)	64	(0)	43	(13)	34	(0)	33	(0)
1984	23	(0)	20	(18)	21	(0)	30	(0)	38	(0)	41	(0)	46	(15)	59	(14)	66	(0)	49	(0)	37	(7)	**	(0)

Table 9. Monthly mean heat content from the surface down to the SST-20°C isotherm (°C x m) for the region 4-14°S off Peru. These means are averages of the monthly means for the three central areas, computed from subsurface temperature profiles. The corresponding number of profiles used in computing each mean (in brackets) is printed to the right of the mean. Means based on zero profile are computed from interpolated values. Asterisks indicate months in which neither observed nor interpolated means were available in all three areas.

Year	Jan		Feb		Mar		Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec	
1951	491	(1)	524	(1)	506	(188)	609	(0)	748	(0)	772	(0)	801	(31)	1,063	(3)	984	(0)	837	(0)	596	(0)	553	(0)
1952	270	(37)	401	(0)	440	(0)	***	(0)	789	(0)	895	(0)	1,154	(122)	1,069	(0)	1,036	(0)	***	(0)	***	(0)	***	(0)
1953	458	(0)	465	(0)	419	(59)	558	(137)	613	(24)	748	(0)	984	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)
1954	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)
1955	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	***	(0)	974	(0)	763	(0)	568	(59)	594	(113)
1956	371	(5)	495	(0)	552	(0)	728	(44)	832	(0)	865	(0)	1,011	(0)	1,000	(0)	1,009	(30)	886	(0)	809	(14)	730	(0)
1957	514	(0)	436	(3)	683	(45)	560	(33)	771	(0)	822	(0)	***	(0)	***	(0)	1,012	(0)	864	(0)	664	(14)	831	(5)
1958	737	(64)	515	(15)	441	(83)	527	(8)	670	(2)	813	(0)	967	(2)	1,003	(0)	1,001	(40)	834	(0)	610	(4)	689	(171)
1959	510	(0)	549	(0)	548	(35)	697	(3)	876	(1)	856	(0)	1,020	(0)	1,012	(0)	1,031	(0)	937	(3)	673	(0)	664	(0)
1960	436	(0)	472	(6)	336	(42)	496	(101)	659	(4)	780	(0)	984	(0)	975	(0)	947	(9)	850	(83)	698	(42)	632	(0)
1961	341	(0)	280	(109)	318	(94)	429	(52)	632	(0)	664	(14)	998	(8)	994	(126)	1,101	(25)	652	(6)	577	(1)	593	(0)
1962	425	(102)	326	(129)	309	(35)	507	(100)	570	(98)	797	(32)	985	(24)	963	(0)	895	(0)	558	(17)	555	(246)	541	(58)
1963	314	(87)	435	(183)	413	(55)	391	(72)	650	(0)	774	(0)	946	(59)	980	(107)	857	(28)	952	(71)	625	(42)	663	(59)
1964	440	(0)	578	(12)	419	(46)	542	(0)	652	(42)	861	(81)	1,034	(3)	1,015	(26)	990	(33)	734	(3)	452	(179)	541	(2)
1965	409	(0)	600	(9)	509	(1)	752	(76)	822	(0)	816	(0)	924	(30)	890	(57)	827	(43)	864	(24)	641	(121)	697	(27)
1966	475	(0)	535	(96)	434	(60)	599	(33)	673	(59)	828	(24)	953	(0)	857	(3)	988	(114)	794	(0)	560	(27)	602	(50)
1967	400	(0)	404	(142)	558	(15)	496	(9)	774	(65)	881	(8)	1,132	(2)	1,079	(79)	1,197	(43)	845	(1)	673	(31)	670	(62)
1968	380	(0)	340	(199)	385	(1)	463	(4)	753	(40)	827	(0)	1,023	(0)	1,040	(0)	1,097	(67)	897	(33)	611	(11)	678	(65)
1969	458	(46)	431	(21)	588	(6)	602	(2)	824	(3)	898	(19)	950	(53)	748	(26)	851	(145)	669	(0)	447	(58)	555	(14)
1970	415	(0)	498	(0)	490	(0)	604	(0)	797	(2)	834	(23)	992	(0)	974	(0)	1,024	(38)	665	(72)	693	(112)	557	(49)
1971	421	(0)	474	(0)	459	(0)	568	(10)	672	(25)	711	(20)	1,014	(0)	1,039	(141)	1,053	(39)	844	(8)	522	(116)	582	(52)
1972	427	(1)	504	(25)	573	(85)	780	(76)	799	(30)	880	(2)	1,130	(45)	921	(17)	1,054	(0)	842	(27)	922	(108)	930	(8)
1973	605	(4)	599	(13)	539	(109)	613	(25)	762	(1)	893	(0)	1,167	(10)	1,117	(23)	1,045	(19)	864	(0)	656	(0)	618	(0)
1974	435	(2)	317	(36)	452	(44)	582	(10)	875	(7)	856	(23)	1,100	(5)	1,024	(5)	1,070	(0)	1,049	(3)	711	(64)	698	(0)
1975	504	(6)	592	(2)	684	(55)	677	(42)	806	(55)	868	(1)	1,095	(0)	1,131	(115)	1,102	(0)	864	(0)	557	(15)	548	(18)
1976	431	(0)	514	(0)	612	(6)	596	(17)	771	(0)	872	(0)	1,127	(38)	1,083	(25)	1,045	(0)	786	(23)	688	(0)	760	(30)
1977	570	(0)	707	(26)	579	(0)	626	(0)	734	(0)	771	(11)	1,019	(0)	1,021	(9)	1,037	(0)	906	(11)	653	(9)	674	(0)
1978	501	(0)	658	(1)	542	(5)	627	(0)	797	(2)	799	(0)	949	(4)	960	(0)	979	(0)	809	(0)	592	(21)	648	(0)
1979	470	(0)	***	(0)	***	(0)	***	(0)	***	(0)	818	(0)	999	(0)	988	(26)	1,009	(0)	828	(0)	623	(0)	564	(8)
1980	462	(0)	605	(4)	447	(17)	593	(0)	759	(0)	849	(0)	1,051	(0)	1,040	(11)	1,027	(0)	838	(0)	***	(0)	***	(0)
1981	438	(0)	430	(0)	303	(21)	519	(0)	727	(0)	***	(0)	***	(0)	***	(0)	993	(0)	815	(0)	594	(35)	776	(19)
1982	494	(0)	525	(5)	488	(35)	596	(24)	768	(0)	854	(0)	1,070	(0)	1,135	(23)	1,117	(0)	1,022	(0)	1,056	(32)	832	(7)
1983	663	(6)	849	(14)	688	(1)	883	(63)	957	(3)	988	(59)	1,067	(50)	1,017	(8)	982	(0)	782	(13)	617	(0)	641	(0)
1984	456	(0)	464	(16)	476	(0)	590	(0)	735	(0)	777	(0)	855	(11)	1,006	(12)	997	(0)	848	(0)	680	(7)	***	(0)

from January through March to about 1,000 $^\circ$Cm from July through September. The between-year standard deviation varies from about 100 $^\circ$Cm in June to about 200 $^\circ$Cm in November and February. The range between extrema varies from 200 to 600 $^\circ$Cm. The autocorrelation function of heat content is 0.5 at lag one and decreases rapidly thereafter, indicating weak persistence with time (Fig. 5D). Along the coast, the long-term monthly means of heat content generally slope downward to the south. For instance, the long-term annual mean heat contents for Area I in the north and Area V in the south are 582 $^\circ$Cm and 843 $^\circ$Cm, respectively. This alongshore variation is a consequence of the deepening of the mixed layer in response to upwelling, which is stronger in the south. The interannual variability of the heat content is highest in areas and months around the edges of the upwelling regime.

Sea Level

Sea level represents a vertical integral of the thermohaline structure over the entire water column. Integrating over the water column has the effect of combining many subsurface processes into a single parameter. Frequently, this combining of factors provides an invaluable indication of large-scale oceanic change. Monthly means and anomalies of sea level at Talara and La Punta (Figs. 1D, 1E and 2D, 2E, Tables 4 and 5) show seasonal and interannual variability similar to that described for SST. Sea level at both coastal stations was variable during the early 1950s, moderately low during the mid-1950s, moderately high for the 1957-1959 El Niño episode, slightly below normal for most of the 1960s (except the 1965 and 1969 warm events when it was above normal), very high during the 1972-1973 El Niño, and variable until 1974.

The annual cycle of sea level is characterized by relatively high levels from February through June and low levels from August through December. The interannual variability is generally high from December through June and low from August through September. Bigg and Gill (1986) showed that the long period response of sea level off Peru separates into a remotely forced component mainly due to zonal winds along the equator to the west, and a locally driven component where sea level slopes to balance the alongshore wind. Their examination of the annual component of sea level indicates that the locally forced component dominates, whereas the remotely forced component plays a major role at semiannual and interannual periods.

Summary and Implications

All of the time series presented show considerable seasonal and interannual variability. Each series had a strong annual cycle, dominated by seasonal shifts from an intensified upwelling regime from May to October to a relaxed upwelling regime in which warm water intrudes from the north from January through March. Contrary to this single peak pattern observed for SOI, SST, sea level, depth to the SST-2°C isotherm, and heat content, deep isotherms, represented by the depth of the 14°C isotherm, had double peaks in their annual cycles. Along the Peru coast, the seasonal variability increased from north to south, with lowest variability associated with weaker upwelling in the north than in the south.

Interannual variations of most of the series were similar, being dominated by remotely-forced El Niño signals. Contrary to this pattern, however, interannual variations of the depth to the SST-2°C isotherm and heat content down to this isotherm were only weakly correlated to El Niño signals. Interannual variations of these two parameters appear to occur at longer periods. Weaker persistence suggests that these two parameters may be dominated by local rather than large-scale processes, such as local wind or heating events. The parameters which were correlated to El Niño signals showed that coastal waters off Peru (4-14°S) were generally cool in the early 1950s, moderately warm during 1957-1959, near normal during 1960-1965, warm in 1965, near normal during 1966-1968, warm in 1969, cool in 1970 and 1971, very warm in 1972, cool during 1973-1975, warm during 1976-1981, extremely warm in 1982-1983 and variable in 1984. La Punta SST was below normal in 1984-1985, but the 14°C isotherm was still depressed.

The warm events described by the above interannual variations represent a general deepening of the thermal structure along the coast as indicated by a depression of the 14°C isotherm. Such depressions cause a change in the slope of the thermal structure normal to the coast and a tendency to increase transport of warm water and associated organisms poleward along the coast. Furthermore, deepening the thermal structure would reduce the biological productivity of the surface waters by reducing the ability of upwelling favorable winds to upwell nutrient-rich water. These depressions of the thermal structure have been shown to occur even during periods of maximum offshore transport, which normally correspond to maximum upwelling and availability of nutrients.

The effects of interannual variability of subsurface temperature on Peruvian anchoveta populations are difficult to access. If one assumed that some combination of factors associated with warming and depression of the thermal structure is detrimental to anchoveta recruitment and/or growth, a scenario of events based on the subsurface variability presented here may be as follows. Heavy fishing pressure in the late 1960s and early 1970s combined with the strong El Niño of 1972, which had a deeply depressed thermal structure, caused a collapse of the anchoveta population. The stock then recovered slightly in 1974-1976 (Avaria 1985) following cool water conditions (upwelling) of 1973-1975 as described by the depression of the 14°C isotherm. However, this slight recovery was subject to continued strong fishing pressure. The moderate 1976-1977 El Niño and the warm, depressed conditions thereafter, especially during the 1982-1983 El Niño, have prevented good recruitment, resulting in very low anchoveta populations. A reversal to cooler conditions since 1983 may be associated with a modest recent recovery of the population. Clearly, the actual ecosystem of the Peruvian anchoveta is much more complicated than this simple scenario suggests. This scenario does, however, illustrate the potential value of multiple environmental time series such as presented in this volume.

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ON THE STANDARD METABOLIC RATES OF TROPICAL TUNAS, INCLUDING THE EFFECT OF BODY SIZE AND ACUTE TEMPERATURE CHANGE

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ABSTRACT

The standard metabolic rates (SMR's) of fishes and the effect of body weight on SMR's are important input parameters to energetics, growth, and population models. This study was undertaken to obtain these data for the tropical tuna species, yellowfin tuna, *Thunnus albacares*, and kawakawa, *Euthynnus affinis*. These data compliment similar SMR measurements from skipjack tuna, *Katsuwonus pelamis*, previously published. The effect of acute temperature change on the SMR of all three species was also determined.

The SMR was estimated by directly measuring the oxygen uptake rate of animals paralyzed with a neuromuscular blocking drug, rather than by the more commonly used method of extrapolation of swimming speed-metabolic rate curves back to zero swimming speed. To test the adequacy of this technique, the SMR's of aholehole, *Kuhlia sandvicensis*, and rainbow trout, *Salmo gairdnerii*, were determined using similar methodology. The SMR's measured in this way were not significantly different from the published SMR's of these species determined by extrapolation of swimming speed-metabolic rate curves back to zero swimming speed.

All three tuna species have very high SMR's, over five times higher than other active teleost species such as salmon and trout. The effect of body size on the SMR is similar in all three tuna species, but the weight specific SMR of tuna decreases more rapidly with increasing body size than in other fishes. Based on SMR's measured at 20° and 25°C, the Q_{10}'s were 3.16, 2.31, and 2.44 for yellowfin tuna, kawakawa, and skipjack tuna, respectively. These are similar to Q_{10} values found for the SMR's of other teleosts.

Tunas can achieve exceptionally high maximum aerobic metabolic rates. This ability requires a complete set of anatomical, physiological, and biochemical adaptations. I hypothesize that one of these adaptations, large gill surface areas, causes tunas to have exceptionally high energy demands even at rest. Tunas' high SMR's are an inevitable consequence of their ability to achieve exceptionally high maximum aerobic metabolic rates.

The standard metabolic rate (SMR) (the metabolic rate of a postabsorptive animal completely at rest) and the effect of body size on SMR are important input parameters to growth, energetics, and population models (e.g., Sharp and Francis 1976; Kitchell et al. 1978). This study was therefore undertaken to obtain these data for yellowfin tuna, *Thunnus albacares*, and kawakawa, *Euthynnus affinis*. These measurements were designed to directly compliment the SMR measurements for skipjack tuna, *Katsuwonus pelamis*, that had been previously published (Brill 1979). The effect of acute temperature change on the SMR of skipjack tuna, yellowfin tuna, and kawakawa was also determined. The effect of acute temperature change, as opposed to the effect of temperature adaptation, is relevant to tuna because of the 5° to 15°C water temperature changes these species normally experience during the daily vertical movements which are a constant feature of their behavior in the open ocean (Dizon et al. 1978; Carey and Olson 1982; Yonemori 1982).

In other teleosts, SMR's have been determined by extrapolating metabolic rate-swimming speed curves back to zero swimming speed (e.g., Brett 1965). Although Graham and Laurs (1982) have successfully measured the metabolic rate of albacore, *T. alalunga*, (a temperate tuna species) swimming in a water tunnel, this methodology is presently not possible with tropical tunas (skipjack tuna, yellowfin tuna, and kawakawa). Attempts to get these species to swim in several prototype water tunnel designs have shown that they will do so for only very short periods (Brill and Dizon 1979 and unpublished observations). As a result, measuring the SMR's of tropical tunas directly in animals paralyzed with a neuromuscular blocking agent is currently the only method available to obtain these data.

To validate this technique, the SMR's of rainbow

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trout, *Salmo gairdneri*, and aholehole, *Kuhlia sandvicensis*, were also measured using paralyzed animals. These two species were chosen because they are available in Hawaii and because there are published data on their SMR's based on extrapolation of swimming speed-metabolic rate curves back to zero swimming speed (Muir et al. 1965; Bushnell et al. 1984).

The SMR of a 1 kg skipjack tuna (412 mg O_2/h, Brill 1979), is almost five times greater than that of a 1 kg sockeye salmon, *Oncorhynchus nerka* (83 mg O_2/h, Brett and Glass 1973). The former measurements were made at 25°C and the latter at 20°C, because 25°C is the upper lethal temperature for salmon (Brett 1972). However, a 5°C temperature difference could not account for this SMR difference because the Q_{10}'s for the SMR's of fishes are generally about 2 (Robinson et al. 1983). The maximum sustainable aerobic metabolic rate (MMR, the metabolic rate at the maximum swimming speed sustainable for at least 1 h) of a 1 kg sockeye salmon at 20°C is 796 mg O_2/(kg·h), whereas 1.8-2.2 kg skipjack tuna at 24°C have been shown to be able to achieve active metabolic rates over 2,000 mg O_2/(kg·h) (Gooding et al. 1981). Although there are no metabolic rate measurements available for tunas at their maximum sustainable swimming speeds, two conclusions are still obvious: 1) skipjack tuna have very high SMR's even when compared with other active equal sized teleosts and 2) skipjack tuna are capable of very high aerobic metabolic rates.

I hypothesize that the high SMR's of tunas are primarily a result of their large gill surface areas (Hughes 1979). In other words, adaptations that permit high maximum sustainable rates of oxygen uptake (i.e., high MMR's) obligate tunas to have high SMR's. Analogous arguments with respect to the resting and maximal metabolic rates of terrestrial vertebrates have been presented by Bennett and Ruben (1979).

MATERIALS AND METHODS

SMR Measurements-Tuna

Live skipjack tuna, yellowfin tuna, and kawakawa were purchased from local fishermen and maintained at the Kewalo Research Facility (Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA). Animal procurement, handling, and maintenance procedures at this facility are described by Nakamura (1972), Queenth and Brill,[2] and Chang et al.[3] Fishes were maintained in outdoor tanks for a few days to over 1 yr before use. Temperature of the seawater supplied to the holding tanks was 25°C (±2). Food was presented daily; however, individuals were not fed for at least 20 h prior to use in an experiment. This allowed sufficient time for gut clearance and for blood glucose level to return to prefeeding levels (Magnuson 1969).

Each experimental animal was removed from its holding tank by dip net and injected intramuscularly with 1-3 mg/kg of the neuromuscular blocking agent Flaxedil[4] (gallamine triethiodide). The animal was quickly returned to its holding tank, and when it could no longer swim, it was immediately rushed into the laboratory and placed in a Plexiglas flow-through box respirometer similar to that used by Stevens (1972). The respirometer was equipped with a movable partition which was placed immediately behind the fish to reduce the respirometer's volume and, thus, reduce the lag time between actual and measured changes in metabolic rate to only minutes (Niimi 1978). Water flow through the respirometer was maintained at 3-7 L/(kg·min) and was measured every 30-60 min by recording the time to fill a 1 L graduated cylinder. Water temperature was controlled by a chiller and freshwater heat exchanger and by a quartz heater mounted in the inflow seawater line. Temperature control was ±0.3°C.

Unlike the previous study on the SMR of skipjack tuna (Brill 1979), the spinal cord was not cut to stop all overt muscular activity. Rather, an 18-gauge hypodermic needle was placed intramuscularly and connected to the outside of the respirometer via a short length of polyethylene tubing. Through this tube, 0.1-0.3 mL doses of Flaxedil were administered when the fish began to show any slight tail movements. To monitor heart rate, electrocardiogram leads were mounted subcutaneously on the ventral body surface. Heart rate was determined by timing the interval between successive beats with a Hewlett-Packard (HP) 5308A frequency counter. Thermistors were used to measure fish muscle and water temperatures. With the aid of an 18-gauge hypodermic needle, a thermistor bead mounted in 0.9 mm diameter polyethylene tubing was inserted into the red muscle immediately adjacent to the spinal column. Thermistor probes were also mounted in the incoming seawater line and in the respirometer box itself. Red muscle and water temperatures were determined by measuring the resistance of the various thermistors with an HP 3456A digital multimeter.

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[4] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Oxygen concentration (milligrams per liter) of the water upstream and downstream of the fish was determined with a dissolved oxygen meter (Yellowsprings Instrument, model 51A) equipped with a Clark-type polarographic electrode oxygen-temperature probe. The probe was normally in the outflow seawater line, but was moved to the inflow seawater line to determine inflow seawater oxygen levels every 30-60 min. The analog output of the oxygen meter was also measured with the HP digital multimeter. An HP 9825A computer was used to control an HP 5930A six-channel relay actuator which permitted the digital multimeter to determine sequentially the resistances of various thermistors and the analog output of the oxygen meter. Seawater oxygen level, red muscle and water temperatures, metabolic rate, and heart rate were calculated and printed by the computer at 5-min intervals.

After being sealed, the respirometer box was covered with black plastic to minimize disturbance to the fish. Temperature of the seawater supplied to the respirometer was maintained at 21°-22°C for the first 1-2 h because reduced water temperature has been shown to help tuna survive after handling (Barrett and Connor 1964). Seawater temperature was then changed to either 20° or 25°C, and the fish maintained at the test temperature until its metabolic rate remained relatively stable for at least 1 h. The SMR was estimated by averaging the last 5-12 metabolic rate measurements. The standard deviations of the metabolic rate measurements used to estimate SMR were <11% of the mean (i.e., SMR) in all cases, and in 70% of the cases, the standard deviations were <5% of the mean.

To determine the SMR at a second temperature, the water temperature was changed to either 20°, 25°, or 30°C, and metabolic rate measurements continued again until the fish's metabolic rate remained stable for 1 h.

SMR Measurements-Aholehole and Rainbow Trout

Aholehole were obtained from Sea Life Park (Waimanalo, HI) and rainbow trout from a commercial fish farmer (through the University of Hawaii, Hilo). The former were maintained in an outdoor tank with running seawater at 25°C (±2) and the latter, in an indoor tank with running freshwater at 15°C (±2). Both species were fed daily, but individuals were not fed for at least 20 h prior to use in an experiment.

The respirometer used for aholehole was essentially identical to that used by Davis and Cameron (1971) and Jones and Schwarzfeld (1974) to measure water flow and gas exchange across the gills of rainbow trout. The aholehole were anesthetized in 1: 10,000-1:30,000 MS222 (Tricaine methanosulfonate). A thin, rubber membrane was sutured around the fish's mouth and sealed with a small amount of tissue glue (Histoacryl, B. Braun Melsungen AG, West Germany). The fish was then placed in a black Plexiglas box that was open at both ends. This box was then placed in a larger tank that was divided into two chambers by a partition with a hole through it. The membrane sealed around the fish's jaws was attached to the edge of the hole and sealed in place with a Plexiglas plate held with stainless steel wing nuts. This system allowed separation of the inspired and expired water, yet allowed the fish to make normal respiratory movements. Water level in the two chambers was maintained by standpipes (constant level drains). Ventilation volume was determined by measuring the water flow rate from the standpipe in the chamber containing the fish. By lowering this standpipe, the fish could be force-ventilated.

Water samples were drawn from the anterior chamber, and from the black Plexiglas box containing the fish, approximately every 15 to 20 min. Water oxygen level was determined with a water-jacketed oxygen electrode (Radiometer, Copenhagen) maintained at 25°C. Metabolic rate was calculated using the oxygen content difference between inspired and expired water and the ventilation volume.

Aholehole were given 2 h to recover from the anesthesia before metabolic rate measurements were begun. A series of metabolic rate measurements were made with the water level in the two chambers even and the fish actively pumping water over its gills, until the its metabolic rate remained relatively stable for at least 1 h. The water level in the chamber containing the fish was then lowered and measurements taken while the animal was being force-ventilated, continuing again until the metabolic rate stablized. Finally, the fish was given 0.1-0.3 mL Flaxedil (intramuscularly) and metabolic rate measurements continued while the animal was paralyzed and force-ventilated. In two cases, the fish was left in the respirometer overnight on forced ventilation to allow the effects of Flaxedil to wear off. Metabolic rate measurements were made again before and after Flaxedil injection the next day. The SMR was calculated as the mean of the last four to six metabolic rate measurements. Water temperature was maintained at 25°C (±0.3) throughout the experiment.

The SMR of rainbow trout was directly determined in the same respirometry box as that used for tunas, using essentially identical methodology, except freshwater was used, inspired and expired water were sampled, and oxygen levels were measured with a water-jacketed Radiometer oxygen electrode.

RESULTS

Effects of Body Size on SMR

The SMR's of 21 kawakawa (0.540-2.153 kg) and 13 yellowfin tuna (0.585-3.890 kg) were determined at 25°C. Regression lines of SMR versus body weight were fitted by Gauss-Newton iteration (Biomedical Computer Programs, Program BMDP 3R), rather than a log-log transformation of the data (Fig. 1). The advantages of the former and disadvantages of the latter method are discussed by Zar (1968) and Glass (1969).

The best fitting allometric equations are

1) Kawakawa:
$$\mathrm{SMR} = 392.5\ (\pm 32.3)\ W^{0.496\ (\pm 0.145)}$$
$$n = 21$$
2) Yellowfin tuna:
$$\mathrm{SMR} = 286.8\ (\pm 26.9)\ W^{0.573\ (\pm 0.116)}$$
$$n = 13.$$

For comparison, the allometric equation relating

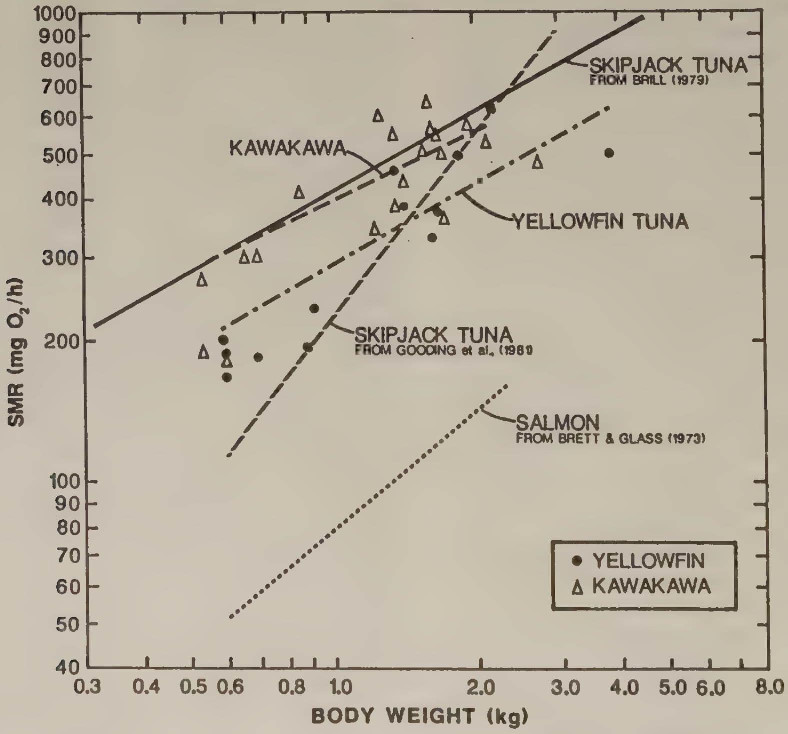

FIGURE 1.—A double logarithmic plot of the standard metabolic rates (SMR) of 13 yellowfin tuna and 21 kawakawa. The lines represent the allometric equations: $\mathrm{SMR} = 286.8\ W^{0.573}$, $\mathrm{SMR} = 392.5\ W^{0.496}$, and $\mathrm{SMR} = 412.0\ W^{0.563}$ for yellowfin tuna, kawakawa, and skipjack tuna, respectively, where the SMR is mg O_2/h and W is body weight in kilograms. The line for skipjack tuna is from Brill (1979). For comparison, the regression lines based on swimming skipjack tuna (Gooding et al. 1981) and for salmon at 20°C (Brett and Glass 1973) are also shown. All tuna data is from fish at 23°-25°C.

SMR and body weight in skipjack tuna is (Brill 1979)

$$\mathrm{SMR} = 412.0\ (\pm 27.1)\ W^{0.563\ (\pm 0.07)}$$
$$n = 33.$$

The SMR is in mg O_2/h and W is body weight in kilograms. The values in parentheses are the standard errors of the parameters.

Effects of Acute Temperature Change on SMR, Heart Rate, and Excess Red Muscle Temperature

A total of 8 kawakawa, 12 yellowfin tuna, and 5 skipjack tuna were subjected to 5°C temperature changes. Most temperature changes were made between 20°C and 25°C, which all fish survived. Ten fish were exposed to 25° and 30°C, but only four survived long enough at 30°C to provide usable data. Because of the expense and difficulty in obtaining live tunas, the latter treatment was not pursued.

The SMR's and mean heart rates at 20°, 25°, and 30°C are given in Table 1. The Q_{10}'s of SMR for water temperatures changes from 20° to 25°C were variable and ranged from 5.82 to 1.39. The mean Q_{10}'s (±95% confidence intervals) were 2.44 ± 0.97, 2.31 ± 0.51, and 3.16 ± 0.93 for skipjack tuna, yellowfin tuna, and kawakawa, respectively.

The range of mean excess red muscle temperatures are given in Table 2. These excess muscle temperatures are lower than those measured in free swimming yellowfin and skipjack tunas (Dizon and Brill 1979). This is as expected because in paralyzed tunas, most of the heat production (i.e., energy consumption) most likely occurs at the heart and gills where the heat would not be retained by the vascular countercurrent heat exchangers.

The SMR of Aholehole and Rainbow Trout

Aholehole, unlike rainbow trout, will not sit quietly in a darkened respirometer box nor stop breathing movements when force-ventilated. Because Flaxedil

TABLE 1.—Effect of temperature on the standard metabolic rate and heart rate of yellowfin tuna, kawakawa, and skipjack tuna.

Species	SMR (mg O_2 h)			Q_{10}		Heart rate (min^{-1})			Q_{10}	
Weight	20°C	25°C	30°C	20°-25°C	25°-30°C	20°C	25°C	30°C	20°-25°C	25°-30°C
Yellowfin tuna										
2.215	470 ± 47	625 ± 53	—	1.77	—	89 ± 1	133 ± 2	—	2.21	—
1.438	258 ± 8	386 ± 21	605 ± 13	2.24	2.46	98 ± 1	146 ± 2	176 ± 1	2.22	1.45
1.635	161 ± 17	330 ± 17	—	4.20	—	81 ± 2	138 ± 2	—	2.89	—
3.890	311 ± 12	501 ± 32	—	2.60	—	57 ± 2	90 ± 2	—	2.49	—
0.704	112 ± 6	184 ± 8	—	2.70	—	99 ± 4	149 ± 1	—	2.26	—
0.877	150 ± 6	193 ± 6	—	1.66	—	77 ± 1	121 ± 3	—	2.45	—
0.599	103 ± 3	166 ± 6	—	2.60	—	73 ± 6	138 ± 8	—	3.55	—
0.595	153 ± 6	187 ± 6	—	1.49	—	74 ± 6	137 ± 5	—	3.41	—
0.585	154 ± 9	199 ± 3	266 ± 10	1.67	1.73	118 ± 1	159 ± 3	200 ± 2	1.82	1.58
1.290	333 ± 4	493 ± 17	—	2.19	—	106 ± 1	160 ± 2	—	2.28	—
Mean:				2.31	2.10				2.56	1.59
Standard deviation:				0.80	0.52				0.56	0.09
Kawakawa										
1.439	258 ± 12	431 ± 19	—	2.79	—	128 ± 1	205 ± 8	—	2.57	—
1.713	331 ± 12	497 ± 11	—	2.25	—	147 ± 2	213 ± 2	—	2.10	—
0.870	170 ± 14	410 ± 27	—	5.82	—	147 ± 4	217 ± 6	—	2.18	—
1.283	379 ± 9	598 ± 25	—	2.49	—	146 ± 14	206 ± 23	—	1.99	—
1.623	363 ± 27	640 ± 23	—	3.11	—	118 ± 4	175 ± 3	—	2.20	—
1.377	—	543 ± 35	761 ± 23	—	1.96	—	200 ± 14	272 ± 27	—	1.85
1.653	309 ± 7	560 ± 34	—	3.28	—	155 ± 1	221 ± 4	—	2.03	—
0.700	195 ± 10	300 ± 11	—	2.37	—	183 ± 4	253 ± 15	—	1.91	—
Mean:				3.16	1.96				2.14	1.85
Standard deviation:				1.23	—				0.22	—
Skipjack tuna										
1.069	140 ± 7	263 ± 22	—	3.53	—	78 ± 28	202 ± 4	—	6.71	—
0.582	214 ± 8	282 ± 6	386 ± 7	1.87	1.87	148 ± 2	237 ± 9	275 ± 20	2.56	1.35
0.425	173 ± 6	226 ± 11	—	1.71	—	122 ± 6	191 ± 5	—	2.45	—
0.448	179 ± 9	211 ± 8	—	1.39	—	134 ± 8	197 ± 3	—	2.16	—
0.629	113 ± 6	217 ± 7	—	3.71	—	145 ± 3	212 ± 3	—	2.14	—
Mean:				2.44	1.87				3.74	1.35
Standard error:				1.09	—				2.11	—

TABLE 2.—Range of mean (±SD) excess muscle temperatures in paralyzed tuna.

Tuna	20°C		25°C		30°C	
	Mean	SD	Mean	SD	Mean	SD
Kawakawa	0.7(±0.2)-1.9(±0.3)		0.5(±0.2)-1.5(±0.3)		[1]1.0(0.1)	
Yellowfin	0.3(±0.2)-1.4(±0.1)		0.0(±0.1)-0.7(±0.2)		0.2(±0.1)-0.4(±0.1)	
Skipjack	0.2(±0.1)-0.6(±0.1)		0.0(±0.2)-1.0(±0.2)		[1]0.6(±0.2)	

[1] Only one fish survived long enough to provide useful data.

stops all movements, all fish showed a decrease in metabolic rate after injection. The decrease ranged from 10 to 52% (mean 36%).

The directly measured SMR's from four aholehole and four rainbow trout paralyzed with Flaxedil are given in Table 3.

DISCUSSION

Adequacy of Directly Measured SMR

Muir et al. (1965) provided a regression equation for SMR versus weight for aholehole adapted to 23°C freshwater, based on extrapolation of swimming speed-metabolic rate curves back to zero swimming speed. The predicted freshwater SMR's based on their regression equation was increased by 75% to account for the higher osmoregulatory costs of seawater adapted animals (Nordlie and Leffler 1975). No correction was made for temperature. As shown in Table 3, in all cases but one, the directly measured SMR's are close to the SMR's based Muir et al.'s data when corrected for seawater adapted animals. With respect to rainbow trout, in all cases but one, directly measured SMR's are within one standard deviation of the SMR's obtained by extrapolation to zero swimming speed for rainbow trout at 15°C obtained by Bushnell et al. (1984). Therefore, directly measuring SMR's in Flaxedil-paralyzed aholehole and rainbow trout yields data that are similar to data obtained by the more widely used method of determining SMR by extrapolation of a swimming speed-metabolic rate curve back to zero swimming speed.

Tropical tuna species such as yellowfin, skipjack, and kawakawa will survive in a swimming tunnel for only short periods of time. Although other methods to control swimming speed (such as weighting and fin clipping, Dizon and Brill 1979; Boggs 1984) have been tried, they have met with only limited success. Therefore, direct measurement of SMR's using Flaxedil-paralyzed animals is for now the only way to obtain these data for tropical tuna species. As the data from aholehole and rainbow trout show, direct measure of SMR's using paralyzed animals yields results similar to that obtained by the more commonly used method of extrapolating swimming speed-metabolic rate curves back to zero swimming speed.

The heart rates (+1 SE, at 25°C) observed in this study were 230+20, 206+36, 132+17/min for skipjack tuna, kawakawa, and yellowfin tuna, respectively. These heart rates are higher than those observed for lightly anesthetized skipjack tuna (Stevens 1972), and are 60 and 39% higher than heart rates measured in skipjack and yellowfin tunas (respectively) that have been immobilized by spinal blockade with lidocaine and are force ventilated (unpubl. obs.). The heart rates measured in Flaxedil-paralyzed animals are, however, within the range exhibited by free-swimming skipjack tuna (80-240 beats/min, Kanwisher et al. 1974). The higher heart

TABLE 3.—Standard metabolic rate of aholehole and rainbow trout.

Oxygen consumption (mg O_2 kg^{-1} h^{-1}) ± SD					
Aholehole			Rainbow trout		
Weight (g)	Measured SMR	Predicted SMR[1]	Weight (g)	Measured SMR	Predicted SMR[2]
65.5	264(±12.2)	118	289	53.3(±3.8)	82.5±(27.4)
80.9	146(±16)	113	401	78.8(±7.0)	82.5±(27.4)
91.2	[3]135/127(±9.9/8.8)	111	403	60.5(±10.9)	82.5±(27.4)
108.5	[3]114/162(±11.1/12.0)	106	568	55.5(±9.9)	82.5±(27.4)

[1] Based on Muir et al. (1965) and corrected for saltwater adapted fish based on Nordlie and Leffler (1975).

[2] From Bushnell et al. (1984), for 250-350 g fish adapted to 15°C. No corrections for the weight dependence of SMR were provided.

[3] SMR determinations made approximately 20 h apart.

rates observed in paralyzed tunas may be due to the vagolytic action of Flaxedil (Grollman and Grollman 1970). However, as the data from aholehole and rainbow trout show, estimating SMR using animals paralyzed with Flaxedil and by extrapolation of swimming speed-metabolic rate curves back to zero swimming speed yield similar results.

Effect of Body Size and Acute Temperature Change on SMR

In Figure 1, it appears that the SMR's of yellowfin tuna are lower than those of skipjack tuna and kawakawa. However, based on the 95% confidence intervals, the heights of the regression lines (at mean body weights) are not significantly different from each other. Based on the 95% confidence intervals, the weight exponents of the regression equations for kawakawa, yellowfin tuna, and skipjack tuna also are not significantly different over the size ranges tested (Fig. 1). In other words, the effect of body weight on the SMR is not significantly different among the three tuna species. The exponent in the allometric equation describing the effect of body size on the SMR of other teleosts ranges from approximately 0.65 to >1 (Winberg 1956; Fry 1957; Beamish 1964; Beamish and Mookherjii 1964; Glass 1969; Brett 1972). The lower values of the exponents for tunas indicate that the weight specific SMR[5] (i.e., mg $O_2/(g \cdot h)$) of tunas decreases more rapidly as body size increases than it does for other teleosts.

Gooding et al. (1981) also estimated the SMR of skipjack tuna. When converted to the same units used in this study (SMR in mg O_2/h and W in kg), the relationship they found for the effect of body weight on SMR was

$$\text{SMR} = 234\ W^{1.19}.$$

The exponent greater than one means that they predict the weight specific SMR to increase with increasing body size. As shown in Figure 1, Gooding et al.'s predicted SMR's are lower than mine for small fish, but exceed my estimates above approximately 2.5 kg body weight because of the large weight exponent.

To estimate SMR, Gooding et al. (1981) used a multiple linear regression equation of the logarithm of metabolic rate versus swimming speed and the logarithm of body weight, and then extrapolated back to zero swimming speed. Their data and extrapolations were based on several groups of different-sized fish swimming at voluntary speeds in a tank respirometer. This methodology is not equivalent to the more conventional one of estimating SMR based on swimming speed-metabolic rate curves that are constructed by forcing one fish, swimming in a tunnel respirometer, to undergo stepwise increases in swimming speed during which the fish remains for at least 1 h at each speed (Brett 1972). Furthermore, Gooding et al. (1981) expressed swimming speeds in body lengths per second. Boggs (1984) has shown that this will cause appreciable bias when fitting multiple linear regression equations because the effect of the body size on active metabolic rate is different at different swimming speeds.

The Effect of Acute Temperature Change on SMR and Heart Rate

As shown in Table 1, the Q_{10}'s (effect of temperature) for the SMR's of skipjack tuna, yellowfin tuna, and kawakawa are the same. They are also close to the Q_{10}'s for SMR's of other teleost species subjected to acute temperature change ($Q_{10} = 2.16$, Moffitt and Crawshaw 1983; $Q_{10} = 2.10$, Boehlert 1978), and for the effect of temperature on SMR where fish were acclimated to each test temperature ($Q_{10} = 2.48$, Ott et al. 1980; $Q_{10} = 1.82$-2.83, Duthie 1982).

This result was not expected since studies on the effect of temperature change on the metabolic rate of isolated red and white muscle samples (Gordon 1968, 1972a, 1972b), volitional swimming speed (Dizon et al. 1978), and preliminary work on active metabolic rate of skipjack tuna showed all three to be unaffected by temperature.

Comparing the metabolic rate (1,052 mg O_2/h, from Gooding et al. 1981) of a 2.0 kg skipjack tuna at its minimum swimming speed (1.4 body lengths/s) to its directly measured SMR (608 mg O_2/h, from Brill 1979), shows that the SMR constitutes 58% of the minimum swimming metabolic rate. Because skipjack tuna's SMR constitutes a large fraction of their metabolic rate at minimum swimming speeds and increases as temperature increases, whereas swimming metabolic rate and volitional swimming speed do not, increases in muscle efficiency (i.e., increases in thrust developed by the caudal propeller per unit of O_2 uptake), reductions in hydrodynamic drag (perhaps due to reduction in water viscosity), or unknown physiological adjustments must occur when ambient temperature increases to keep active metabolic rate temperature independent.

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[5] If the allometric equation to describe the effect of body size on whole body standard metabolic rate (SMR) is $\text{SMR} = aW^b$, then the corresponding equation to describe weight-specific SMR versus body weight is $\text{SMR}/W = aW^b/W$ or $\text{SMR}' = aW^{b-1}$; where SMR' = weight-specific SMR, W = body weight, and a and b are fitted parameters.

The effect of water temperature (20°-25°C) on heart rate was variable (Q_{10}'s ranged from 6.71 to 1.82). The mean values (±95% confidence intervals) of 3.74 (±1.9), 2.56 (±0.35), 2.14 (±0.17) for skipjack tuna, yellowfin tuna, and kawakawa, respectively, are not significantly different from each other and are close to the Q_{10} (2-3) found for the effect of temperature on the heart rate of lingcod, *Ophiodon elongatus*, (Stevens et al. 1972).

Why Are The SMR's of Tunas So High?

Also shown in Figure 1 is the SMR-body weight relationship for sockeye salmon at 20°C, taken from Brett and Glass (1973). Even with the differences in the slopes of the lines, it is still apparent that tunas have remarkably high SMR's. In the following paragraphs, I argue (as did Stevens and Neill 1978; Stevens and Dizon 1982) that tunas are "energy speculators", gambling high rates of energy expenditure against high rates of energy return. I also hypothesize that tunas' physiology and anatomy have evolved to increase maximum sustainable (i.e., aerobic) metabolic rates (MMR's) and that high SMR's are an inevitable consequence of this ability. In other words, high SMR's are a result of anatomical and physiological adaptations (primarily large gill surface areas) associated with high MMR's. Tunas have high MMR's and high SMR's, whereas sluggish bottom-dwelling flatfish (e.g., *Platichthys fleusus*) have low MMR's and low SMR's (Duthie 1982). Active fish like salmon have MMR's and SMR's intermediate between these two extremes (Brett 1972).

Advantages of High Maximum Metabolic Rates

Tunas live in the open ocean, an environment which provides no shelter and where patches of forage are widely scattered (Sund et al. 1981). In this environment, high sustainable swimming speeds (i.e., high MMR's) enable tunas to travel quickly between food patches and to search large volumes of water in the least amount of time. Also, tunas have been shown to have very high rates of digestion (Magnuson 1969), which is advantageous for species that must be able to fully exploit a food patch whenever one is found. Since digestion is an energy consuming process, high rates of oxygen delivery and blood flow are required for high rates of digestion.

Because the pelagic environment provides tuna no place to hide and rest while repaying an oxygen debt, the ability to quickly metabolize lactate is also advantageous. High MMR's therefore allow tuna to rapidly repay an oxygen debt when one is accumulated. Tuna's only defense against predators such as blue marlin, *Makaira nigricans*, is presumably a burst of maximum (i.e., anaerobic) swimming. Prey capture by tunas also must involve some high speed swimming. Coulson (1979) has argued that the ability to achieve high rates of anaerobic glycolysis allows vertebrate ectotherms to successfully compete with vertebrate endotherms, which are capable of much higher rates of aerobic metabolism. However, most vertebrate ectotherms, whether terrestrial or aquatic, must spend long quiescent periods to metabolize lactate (Coulson et al. 1977). Yet tunas have the ability to metabolize some of the highest muscle lactate levels ever recorded in vertebrates in only a few hours (Barrett and Connor 1964; Hochachka et al. 1978). Other teleosts may take as long as 24 h to recover from severe exercise even though they accumulate lower white muscle lactate concentrations (Black et al. 1961; Wardle 1978). Tunas' vascular heat exchangers appear to also aid the rapid movement of lactate from the white muscle where it is produced to the red muscle where it is presumably metabolized (Stevens and Carey 1981).

Although using different terminology, McNab (1980) citing terrestrial vertebrates and Pauly (1981) citing fishes, both argue that given certain constraints, high MMR's are advantageous because rates of somatic and gonadal growth are dependent upon rates of delivery of oxygen and substrate to the tissues. Indeed, Pauly (1981) has shown that the growth rates of fishes are proportional to, and perhaps controlled by, gill surface area. Furthermore, he suggests that it is maximum rate of oxygen delivery to the tissues, rather than food supply, that limits growth rates and that species like tunas, which have the largest gill surface areas, have the highest growth rates. Koch and Wieser (1983) have shown that fish reduce activity levels during periods of gonadal growth. Tunas cannot make this trade off. For tunas, it is probably necessary to maintain a high rate of activity during gonadal synthesis which, in turn, requires respiratory and cardiovascular systems capable of delivering oxygen and metabolic substrates to the tissues at high rates.

Adaptations of Tunas For Achieving High Maximum Metabolic Rates

In a series of studies on the MMR's in land mammals (see Taylor and Weibel 1981, and the papers that follow), pulmonary diffusing capacity, mitochondrial volume and capillary density in muscles were shown to be limiting factors in achieving high MMR's. From these studies Weibel et al. (1981) proposed that, at maximum rates of aerobic metabolism, there is no excess capacity at any level in the respiratory chain. In other words, to achieve high MMR's, a complete series of anatomical/physiological/biochemical adaptations must be present. And, as shown in Table 4, these adaptations are present in tunas.

TABLE 4.—Adaptations of tunas for high maximum metabolic rates.

Large gill surface areas	Muir and Hughes 1969
Thin secondary lamella in the gills	Muir and Brown 1971
High hematocrit, high hemoglobin levels (i.e., high blood O_2 carrying capacity)	Klawe et al. 1963; Jones et al. 1986
High maximum cardiac output	Poupa and Lindstrom 1983
Elevated muscle temperatures	Stevens and Neill 1978 Stevens 1982
High muscle myoglobin levels	George and Stevens 1978 Stevens and Carey 1981
High muscle mitochondrial density	George and Stevens 1978 Hulbert et al. 1979
High muscle capillary density	Hulbert et al. 1979
High muscle aerobic enzyme activity levels	Guppy et al. 1979

One of tunas' adaptations for high MMR's are gills with large respiratory surface areas. However, high rates of oxygen uptake are inexorably linked with high osmoregulatory costs, since gills that permit high rates of oxygen uptake must also permit high rates of water and ion movements. This is especially true in marine fishes like tunas where seawater and blood osmolality are approximately 1,000 and 400 mosm, respectively (Bourke 1983). Rao (1968), Farmer and Beamish (1969), Nordlie and Leffler (1975), and Furspan et al. (1984) estimated that the cost of osmoregulation can account for 27 to 50% of the SMR. The gills are a main osmoregulatory effector organ (Evans 1979), and Daxboeck et al. (1982) found that gill tissue respiration alone can account for 27% of the SMR in trout. The SMR, therefore, is obviously strongly influenced by osmoregulatory cost, which in turn is strongly influenced by gill surface area. Ultsch (1973, 1976) came to a similar conclusion after finding that the SMR's of aquatic (i.e., gill breathing) salamanders were controlled by respiratory (i.e., gill) surface area.

Muir and Hughes (1969) measured the total secondary lamellar gill surface (i.e., respiratory) area in skipjack tuna, yellowfin tuna, and bluefin tuna, *Thunnus thunnus*. They found total secondary lamellar areas for 1 kg tunas to be an order of magnitude or more larger than 1 kg bass or roach. Also, they found gill areas were proportional to body weight and the exponent to be 0.85 for the combined data from the three tuna species. This exponent is significantly different from the exponents I found for the effect of body weight on SMR's. It appears that in tunas, the SMR is not strictly determined by secondary lamellar surface area, although high osmoregulatory costs are most likely the main cause of tunas' high SMR's. Also, the difference between the effct of body size on SMR and gill respiratory area implies that larger tunas have greater scope of activity than smaller fishes, as has been shown to occur in other teleosts (Hughes 1984).

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PREVALENCE AND EFFECTS OF INFECTION OF THE DORSAL AORTA IN YELLOWFIN TUNA, *THUNNUS ALBACARES*, BY THE LARVAL CESTODE, *DASYRHYNCHUS TALISMANI*

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ABSTRACT

Approximately 60% of small (<3 kg) yellowfin tuna, *Thunnus albacares*, caught near the Hawaiian Islands carry the plerocercoid (larval) stage of the cestode (tapeworm), *Dasyrhynchus talismani*, in their anterior dorsal aortas. Because the worms and the resultant host inflammation appear to occlude the vessel almost totally, we assumed that the parasite could increase natural mortality rates. Tuna could be limited in their ability to capture prey and therefore should show evidence of long- or short-term food deprivation. We measured body weight, fork length, liver weight, heart weight and, in fish captured from one school, RNA/DNA ratios (a measure of short-term growth rate), and otolith weight (a measure of long-term growth rate) from parasitized and unparasitized fish. We found no significant differences between infected and uninfected fish nor any evidence of starvation in infected fish. How small yellowfin tuna remain apparently unaffected by the parasitic occlusion of their dorsal aorta remains to be demonstrated.

We also examined changes in incidence of infection in small yellowfin tuna caught between February 1985 and March 1986 as well as the prevalence in large (>45 kg) fish. Large yellowfin tuna were rarely parasitized (5.2%) in the dorsal aorta, but showed a high rate (>80%) of infection within other major arteries. The prevalence in small fish varied dramatically with season, dropping suddenly from 66% in June-July 1985 to 11% in August-September 1985. Unparasitized fish caught during August-September 1985 showed significantly higher condition factors, relative heart weights, and relative liver weights than did unparasitized fish caught at other times of the year. We hypothesize that the sudden decrease in prevalence was due to influx of a separate group of small yellowfin tuna into the Hawaiian fishery. We believe that this parasite may therefore serve as a marker for tracing the movements of small yellowfin tuna into and out of specific fisheries or areas.

During a series of experiments that involved catheterization of the anterior dorsal aorta of small (1-3 kg) yellowfin tuna, *Thunnus albacares*, we discovered that approximately 60% of the experimental fish had this blood vessel infected with parasites. The parasites were white, round (2-4 mm in diameter), often more than 4 cm long, and usually folded repeatedly. As a result of the parasites and the tissue inflammation that develops as part of host immune response, the lumen of the infected aortas appeared almost totally occluded. Because all the blood to the internal organs and swimming muscles must flow past this occlusion, we assumed the parasite could be a major factor contributing to the natural mortality of small yellowfin tuna.

The first demonstration of a dorsal aorta parasite in yellowfin tuna was by Kishinouye (1923), who stated, "Often a species of nematod [sic] is found in the dorsal aorta of *Neothunnus macropterus* [now *Thunnus albacares*]; the parasite causes the tissues of the canal to become thick and tough, giving it at the same time a yellowish tint." Other investigators described intravascular parasites from the branchial vessels and arteries serving the stomach, liver, spleen, pyloric caecum, and gall bladder of this species (Baudin Laurencin 1971). The parasites have been described simply as the plerocercoids (larval cestodes) (Chen and Yang 1973), identified to the family Dasyrhynchidae (Ward 1962), or as the species *Dasyrhynchus talismani* (Baudin Laurencin 1971).

Intravascular infection by plerocercoids has been reported from yellowfin tuna caught in the western Pacific (Chen and Yang 1973), eastern Atlantic (Baudin Laurencin 1971), Gulf of Mexico (Ward 1962), and now central Pacific (this report). Infection rates have been reported to be as high as 100% (Baudin Laurencin 1971). If all re-

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ports involve the single parasite species, *D. talismani*, this parasite is both common and ubiquitous.

Because of the apparent vessel blockage by parasites and tissue inflammation, we hypothesized that infected fish would be severely activity limited and not function well as predators. If so, infected fish should show evidence of short- and/or long-term food deprivation, including lower relative condition factors, smaller livers, and slower long- and short-term growth rates (Bulow 1970; Pollard 1971, 1973; Bulow et al. 1981). We also expected blockage of the dorsal aorta to cause increased blood pressures, increased cardiac work, and therefore cardiac hypertrophy (Poupa and Ostadal 1969).

To test our hypotheses, we measured fork length, body weight, liver weight, and ventricle weight from parasitized and unparasitized fish. We also determined RNA/DNA ratios as a measure of the parasite's effects on short-term growth rates (Bulow 1970; Bulow et al. 1981), and relative otolith weights as a measure of the parasite's effects on long-term growth rates. Since otolith weights are linearly related to a fish's chronological age (Boehlert 1985), fish that are older at a given body size should have relatively heavier otoliths. We also recorded the prevalence of infection in small (<3 kg) and large (>45 kg) yellowfin tuna, and in skipjack tuna, *Katsuwonus pelamis*, kawakawa, *Euthynnus affinis*, and bigeye tuna, *T. obesus*. Additionally, monthly prevalence in small yellowfin tuna was noted.

To measure directly the effect of the occlusion caused by the parasites and host inflammation, we used an in vitro perfusion test. We measured the pressure required to push various saline flow rates down the dorsal aorta in freshly dead infected and uninfected fish.

MATERIALS AND METHODS

Sampling Procedures

The small tunas (0.2-3 kg body weight) used in this study were captured at sea near Oahu, HI, returned alive to be held in shoreside tanks at the Kewalo Research Facility (National Marine Fisheries Service, Southwest Fisheries Center Honolulu Laboratory), or sacrificed at sea and held on ice. During necropsy, fork length and body weight were measured, ventricles and livers were removed, blotted dry, and weighed to the nearest 10 mg. Only those fish in captivity for 3 days or less were included in the data for condition factor, and relative heart and liver weights. Large yellowfin tuna (>45 kg body weight) were examined at the Honolulu Fish Auction for the presence of dorsal aorta parasites while the fish were being prepared for sale. All fish were examined within 24 hours of death.

Thirty-five live yellowfin tuna, from one school, were caught 15 January 1986 and transported alive to the Kewalo Research Facility. Immediately upon arrival, the animals were sacrificed, weighed, and measured. Lateral white muscle samples were taken within 4 minutes of death and immediately frozen on dry ice. These samples were subsequently used for measurement of RNA/DNA ratios using the Schmidt-Thannhauser procedure as described in Murno and Fleck (1966). The ventricles and livers of the fish were also removed, blotted dry, and weighed to the nearest 10 mg. Sagittal otoliths were removed, cleaned, dried, and weighed to the nearest microgram.

Parasites for species identification were obtained most often from the major artery within the spleen of large (>45 kg) yellowfin tuna. After being removed from a surrounding capsule, parasites were placed in tap water until the holdfasts everted.

For histological examination, sections of dorsal aorta were fixed in 10% buffered formalin and processed by routine laboratory procedures. Tissue sections were stained with hematoxylin and eosin.

Direct Measurement of Pressure-Flow Relationships in the Anterior Dorsal Aorta

To quantify blockage, we choose to measure the pressures required to push various flow rates of saline through the anterior dorsal aorta of infected and uninfected fish. The dorsal aorta of freshly killed fish was exposed from the confluence of the efferent arteries of the first and second gill arches to the point where it enters the first hemal arch. All efferent and afferent vessels were tied off except for the confluence of the efferent arteries from either the left or right first and second gill arches. This portion of the vessel was cut and a short length of flared polyethylene tubing (PE160, 2.4 mm OD) inserted. The dorsal aorta was also transected at the point where it entered the first hemal arch to allow the saline perfusate to flow out. Parasites were never found posterior to this point. Saline perfusion pressures, at various constant flow rates provided by an infusion pump, were recorded via a Uonix[4] pressure transducer.

Calculation of Relative Condition Factor and Relative Organ Weights

Use of relative condition factor, and relative organ and otolith weights allow groups of fish containing individuals of a range of body sizes to be directly compared (Pollard 1972). Using data from unparasitized fish, regressions of body weight (g) on fork length (cm), liver weight (g) on body weight (g), and heart weight (g) on body weight, were fitted by a least squares technique to the exponential equation:

$$Y = a \cdot X^b$$

using a log-log transformation of the data. Relative condition factor and relative organ weights for individual fish were calculated using the regression parameters (a, b) with the equation:

$$K = W/a \cdot X^b.$$

For relative condition factor, W = body weight and X = fork length. For relative organ weights, W = liver or heart weight, and X = body weight.

The relationship of otolith weight (mg) to body weight was found best fit with the simple linear regression:

$$Y = a + (b \cdot X).$$

Relative otolith weights were therefore calculated using the equation:

$$K = W/(a + b \cdot X)$$

where W = otolith weight and X = body weight.

A relative condition factor <1 indicates that an individual is lighter for its fork length than predicted based on data from unparasitized fish. Similarly, a relative liver or heart weight <1 indiates a smaller liver or heart for a given body size than that found for unparasitized fish. A relative tolith weight >1 means that an individual expeienced a relatively slower long-term growth rate (i.e., is relatively older for a given body size and therefore has a larger otolith).

RESULTS

Identification of the Parasite

Tapeworms (class: Cestoda, order: Trypanorhyncha) can be identified to species based on scolex morphology and tentacular hooks (onchotaxy), mature segments are not required. The larval cestodes recovered from the yellowfin tuna during this study showed proboscis chainettes flanked by a single row of intercalary hooks, a characteristic that distinguishes *Dasyrhynchus talismani* from its congeners.

This parasite was originally described from five mature worms removed from the spiral valve of *Galeus glaucus* (= *Prionace glauca*, the blue shark) off Cape Verde, West Africa (Dollfus 1935). *Dasyrhynchus talismani* has also been reported in the Pacific from *Carcharinus longimanus* (Heinz and Dailey 1974). All other reports describe plerocercoids from the vascular systems of teleost fishes (Bussieras and Aldrin 1965; Baudin Laurencin 1971; Chen and Yang 1973).

Prevalence of Infection by Host Species, Fish Size, and Season

A total of 53 skipjack tuna, 27 kawakawa, 10 bigeye tuna, and 470 yellowfin tuna were examined for the presence of parasites. We found only yellowfin tuna to be infected.

Infection in yellowfin tuna varied with size class. We found a significantly lower incidence of dorsal aorta infection in large fish. Of 220 individuals weighing 0.21 to 2.7 kg, 48% were infected, while of 250 fish weighing more than 45 kg, only 5.2% carried the parasite in their dorsal aortas. Viscera of a small subsample (N = 8) of the larger fish were examined and indicated that in larger fish the parasite infects (in the order of prevalence) the major arteries of the spleen, intestinal caeca, liver, mesenteries, and lateral blood vessels. Fish in intermediate size classes were not available for this study. Fish >3 kg do not survive the trip from the fishing grounds to the Kewalo Research Facility and are therefore not normally captured by commercial fishermen for return to the laboratory. Fish <45 kg are not common at the Honolulu Fish Auction where they could be examined during normal processing. The purchase of intermediate-sized yellowfin tuna specifically for this study (yellowfin tuna intended for market cannot be necropsied and then sold) was prohibitively expensive.

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[4] Reference to trade names does not imply endorsement by the ational Marine Fisheries Service, NOAA.

Infection of yellowfin tuna appears to vary seasonally. Figure 1 shows changes in prevalence of dorsal aorta infection in small (<3 kg) yellowfin tuna captured between February 1985 through March 1986. Prevalence remained stable for approximately 6 months during the winter through early summer. Then in late summer of 1985, prevalence dropped dramatically from 66 to 11%. Beginning in October 1985, prevalence increased steadily, reaching 39% in February-March 1986, the last months for which data are available.

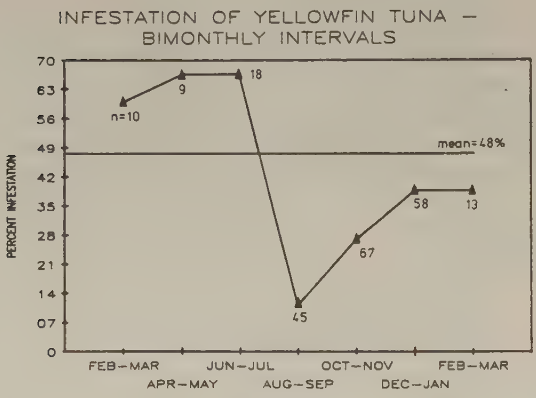


FIGURE 1.—Prevalence (percent infection) of the dorsal aorta by the plerocercoid stage of the cestode *Dasyrhynchus talismani* in small (0.3-3 kg) yellowfin tuna caught near the Hawaiian Islands from February 1985 to March 1986.

Pathology

In infected fish, the anterior dorsal aorta was partially to nearly completely occluded by a parasitic embolus which contained one to several larval cestodes. Figure 2a shows this vessel in a moderately infected yellowfin tuna. Parasites and a small amount of host inflammation are evident in the anterior end (to the right). A normal portion of vessel, with a smooth wall, is seen to the left. Figure 2b shows the anterior dorsal aorta from a very heavily infected fish.

Histological examination revealed that parasitic emboli were primarily composed of larval cestodes, mononuclear cells with eosinophilic granules (presumed to be eosinophils), epitheloid cells (histocytes), fibroblasts, and collagen fibers (Fig. 3). Larval cestodes within the dorsal aorta were associated with a chronic severe endarteritis and, to a lesser extent, mesoarteritis. In heavily infected fish, collapsed channels were commonly found within emboli. Undoubtedly these channels expanded in life with increases in intraluminal blood pressure to allow blood to flow through the vessel. Necrotic worms were also seen, suggesting that the host's defense system was at least partially capable of killing the larvae located in the dorsal aorta.

Infection of other arteries was usually by one, or at most two, larger parasites which were never seen to be folded. These parasites had a bulbous anterior end which always pointed downstream. No evidence of host immune response was observed when the parasites were in vessels other than the dorsal aorta.

Effect of Infection on Measures of Physiological Fitness

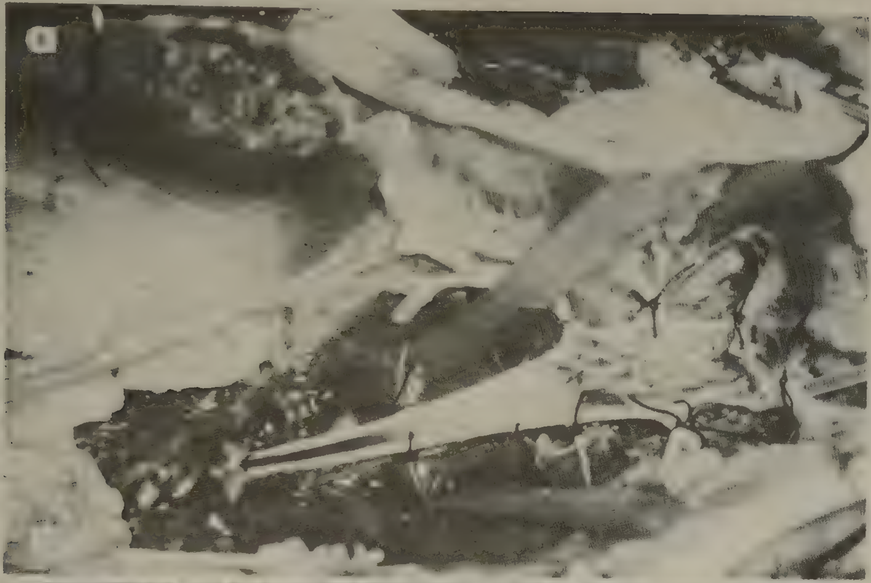
Mean (±1 SD) relative condition factor and mean (±1 SD) relative organ weight data are given in Table 1 for the fish sampled between May 1985 and September 1986. Table 2 lists the same parameters plus mean relative otolith weight, and mean RNA/DNA ratio for fish sampled from the single school captured on 15 January 1986. Means were compared with Student's two-tailed *T* test, with $P = 0.05$ taken as the minimum level for statistical significance.

Examination of data from all the fish caught May 1985-September 1986 reveals statistically significant differences in relative liver and heart weights for parasitized and unparasitized fish. On the average, parasitized fish, have 15% smaller livers, and 9% *smaller* hearts than unparasitized fish. Relative condition factors were not significantly different. When data from fish coming from the single school are examined, there are no statistically significant differences in these three parameters, relative otolith weight, or in RNA/

TABLE 1.—Relative condition factor, relative liver weight, and relative heart weight, of yellowfin tuna sampled between May 1985 and September 1986.

Fish	Mean (±SD) relative condition factor	Mean (±SD) relative liver weight	Mean (±SD) relative heart weight
Uninfected	1.00 (±0.10) *N* = 109	1.02 (±0.22) *N* = 82	1.01 (±0.18) *N* = 88
Infected	0.976 (±0.057) *N* = 35	0.867 (±0.098)* *N* = 22	0.919 (±0.085)* *N* = 32

*Uninfected and infected groups different at $P = 0.05$ level.



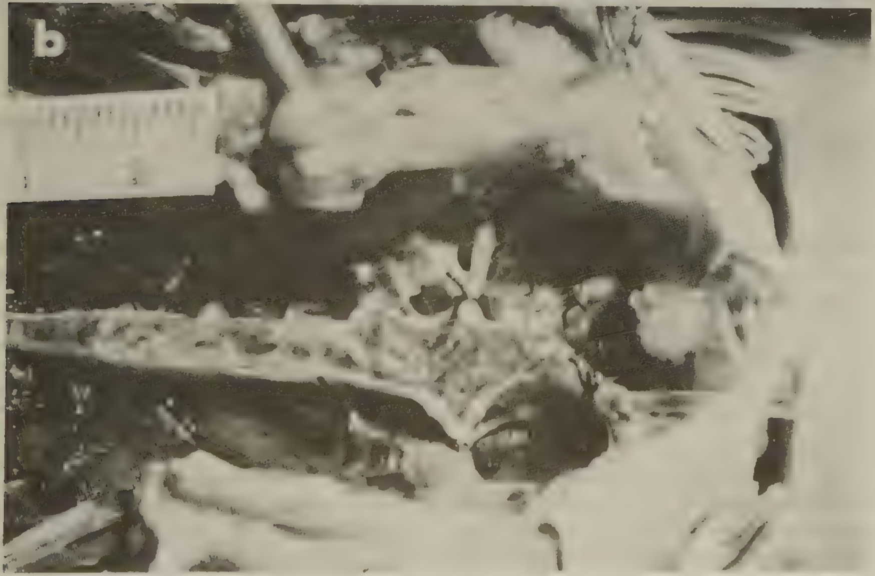


FIGURE 2a.—The anterior dorsal aorta of a moderately infected yellowfin tuna. In the anterior end of the vessel (to the right) are parasites and host inflammation.

FIGURE 2b.—The anterior dorsal aorta of a heavily infected yellowfin tuna. The vessel's lumen is all but occluded by parasites and host inflammation. Ruler divisions are in mm.

TABLE 2.—Relative condition factor, relative liver weight, relative heart weight, relative otolith weight, and RNA/DNA ratio of yellowfin tuna sampled 15 January 1986.

Fish	Mean (±SD) relative condition factor	Mean (±SD) relative liver weight	Mean (±SD) relative heart weight	Mean (±SD) relative otolith weight	Mean (±SD) RNA/DNA ratios
Uninfected	1.00 (±0.04) *N* = 23	1.00 (±0.08) *N* = 23	1.00 (±0.06) *N* = 23	1.00 (±0.04) *N* = 12	28.9 (±8.9) *N* = 21
Infected	0.995 (±0.035) *N* = 12	1.00 (±0.07) *N* = 12	0.975 (±0.074) *N* = 12	0.980 (±0.058) *N* = 8	33.1 (±11.1) *N* = 10

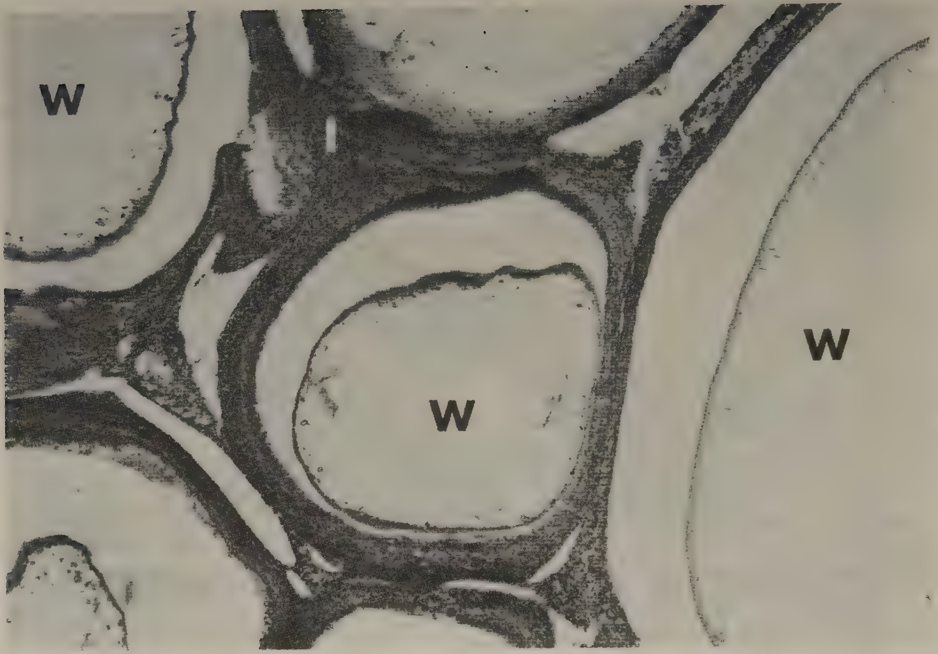


FIGURE 3.—Photomicrograph of a cross section of the dorsal aorta containing parasites and host inflammation of a heavily infected yellowfin tuna. The host inflammation (I) and cross sections of the parasites (W) can be easily differentiated. Hematoxylin and eosin stain.

DNA ratios. RNA/DNA ratios were compared directly (rather than by calculating relative RNA/DNA ratios) because they were found not to be correlated with body weight (correlation coefficient = 0.04).

Data from *unparasitized* fish collected in August and September 1985 were analyzed separately from all remaining *unparasitized* fish. This was done because we found dramatically lower rates of infection (11%) during those 2 months than during the preceding 2 months (67% infected) and assumed this to be due to an influx of a new group of small yellowfin tuna into the Hawaiian fishery. New regression parameters for body weight on fork length, heart weight on body weight, and liver weight on body weight were calculated using data from unparasitized fish excluding those caught during August-September 1985. Mean relative condition factors and relative organ weights were then recalculated.

Table 3 shows mean relative condition factors, mean relative liver weights, and mean relative heart weights for unparasitized fish captured during August and September 1985, unparasitized

TABLE 3.—Relative condition factor, relative liver weight, and relative heart weight from uninfected yellowfin tuna sampled during August and September 1985, from all other uninfected yellowfin tuna, and all infected fish.

Group	Mean (±SD) relative condition factor	Mean (±SD) relative liver weight	Mean (±SD) relative heart weight
August-September 1985 uninfected fish	1.11 (±0.08)* *N* = 36	1.24 (±0.28)* *N* = 35	1.22 (±0.18)* *N* = 36
All other uninfected fish	1.00 (±0.09) *N* = 73	1.01 (±0.17) *N* = 47	1.00 (±0.09) *N* = 52
Infected fish	1.01 (±0.06) *N* = 35	0.937 (±0.102) *N* = 22	1.00 (±0.09) *N* = 32

*Uninfected groups different at $P = 0.01$ level.

fish captured at all other times of the year, and all parasitized fish, based on the new regression parameters. The two groups of *unparasitized* fish show statistically significant differences in all three. Fish caught during August and September were on the average 11% heavier at a given body size (i.e., relative condition factor = 1.11), had livers an average of 23% heavier, and had hearts an average of 22% heavier than those unparasitized fish captured at other times of the year. When unparasitized fish, excluding those caught during August and September, are compared with parasitized fish, there are now no statistically significant differences in mean relative condition factors, mean relative liver weights, or mean relative heart weights. The data from unparasitized fish captured in August and September, when included in the complete data set, are therefore responsible for the observed differences in relative heart and liver weights between infected and uninfected fish seen in Table 1.

In Vitro Perfusion of the Dorsal Aorta

Three parasitized and five unparasitized fish, ranging in weight from 0.915 to 2.666 kg, were used in this series of experiments. The intensity of infection was subjectively classified as slight, moderate, or heavy. Perfusion pressures were normalized to a 1 kg fish weight by dividing the observed pressures by the reciprocal of body weight, in kilograms. Moderately and heavily infected fish showed higher perfusion pressures at a given flow rate than did unparasitized animals (Fig. 4). While no data are available on the normal cardiac outputs and blood pressures in swimming yellowfin tuna, restrained and lightly anesthetized yellowfin tuna have cardiac outputs of approximately 40-60 mL/kg and dorsal aorta blood pressures of 50-70 mm Hg (D. R. Jones and R. W. Brill, unpubl. obs.). Figure 4 shows that at normal cardiac outputs, the apparent occlusion of the dorsal aorta caused by the parasites and host inflammation is indeed real and should cause moderately and heavily infected fish to have excessively high blood pressures, high cardiac energy demands and presumably reduced fitness.

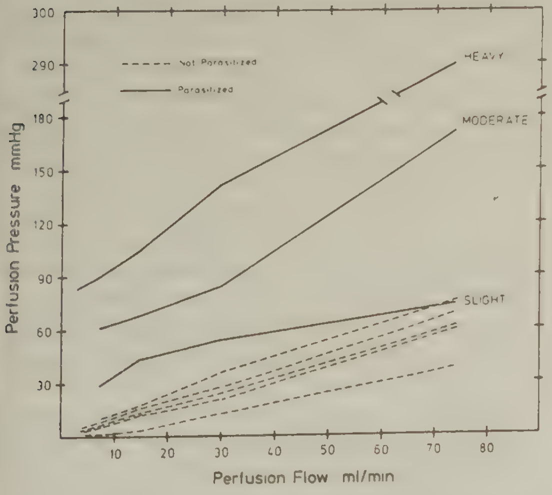


FIGURE 4.—In vitro pressure required to pump various rates of saline down the dorsal aorta of parasitized and unparasitized yellowfin tuna. The fish ranged in size from 0.915 to 2.666 kg. Data have been normalized to a body weight of 1 kg.

DISCUSSION

Prevalence of Infection by Species, Size, and Season

Our data indicate that in Hawaiian waters *D. talismani* is limited to yellowfin tuna. However, *D. talismani* has been reported to occur in Atlantic bigeye tuna (Bussieras and Aldrin 1965). Since we examined relatively few individuals of this species, we cannot rule out the occurrence of this parasite in bigeye tuna in the central Pacific.

Skipjack tuna, bigeye tuna, kawakawa, and yellowfin tuna often occur simultaneously in the same areas and show a great overlap in prey species (King and Ikehara 1956; Waldron and King 1963). It is therefore unlikely that host specificity is attributable to only yellowfin tuna ingesting the intermediate host, which is not known but is most likely a small crustacean (Deardorff et al. 1984). Host specificity could arise if the procercoid of *D. talismani* is not stimulated or is unable to penetrate the gut wall of tuna species other than yellowfin tuna, or that species of tuna other than yellowfin are capable of immune rejection (Orr et al. 1969).

The reasons for the dramatic decrease in incidence of dorsal aorta infection in large (>45 kg) yellowfin tuna are unknown. Possible reasons include procercoids ingested less frequently by larger animals, host destruction of the parasite, increased mortality of parasitized fish, or movement of the parasite out of the dorsal aorta into other major arterial vessels. Of these alternatives, increased mortality of infected fish seems unlikely.

While we did not demonstrate directly the preence of antibodies against the parasite, several histological cross sections show worms in stages of degeneration, and host destruction of larval and adult cestodes has been shown in other teleosts (Kennedy and Walker 1969; Smith 1973; MacKenzie 1975). Examination of a small number of pyloric caeca, liver, spleen, lateral arteries, and stomach vasculature of large yellowfin tuna (>45 kg) showed >85% infection, suggesting 1) that the parasite may move out of the dorsal aorta into other large arteries as yellowfin tuna grow, 2) that the host response to the parasite may be less vigorous in vessels other than the dorsal aorta, and/or 3) that the parasite may preferentially select other vessels in larger fish. Baudin Laurencin (1971) found a decrease in branchial artery infection of yellowfin tuna with increasing body size, but no change in rates of infection of abdominal vessels.

The change in the rate of infection seen in August and September 1985 in small yellowfin tuna (Fig. 1) is, we believe, due to a large influx of uninfected fish into the Hawaiian fishery. Although we have no direct corroborating evidence, such as increased catch per unit effort for this size yellowfin tuna at that time, Tester and Nakamura (1957) have shown that there are repeated influxes of small yellowfin tuna into areas near the main Hawaiian Islands during late summer and early fall. Furthermore, the dramatic differences seen in relative condition factors, relative liver weights, and relative heart weights between unparasitized fish caught during August-September 1985, and the remaining unparasitized fish, clearly imply that the former group had a different history.

We have no evidence nor are we hypothesizing that these groups come from genetically isolated subpopulations. We do believe, however, that the two groups were separate most likely since hatching. We do not know the maximum lifespan of the dorsal aorta parasite, but one yellowfin tuna killed after 172 days in captivity at the Kewalo Research Facility was parasitized. Since fish in captivity are fed only frozen food and their tanks are supplied with filtered seawater (Queenth and Brill[5]), it is unlikely this fish became infected after capture. Yellowfin tuna of the 1-3 kg size range are about 270-360 days old (Uchiyama and Struhsaker 1981) and therefore could have carried the parasite most of their lives.

The slow increase in prevalence from October 1985 through March 1986 remains to be explained, but could be due to emigration of the new group of yellowfin tuna out of the Hawaiian fishery or slowly increasing infection of the new group. This latter explanation implies higher prevalence of the parasite around islands which could be due either to a greater number of final (shark) or intermediate hosts around islands.

Pathology

The severe enarteritis associated with *D. talismani* infection suggests that the parasite is recognized by the fish's defense system as foreign material in the dorsal aorta. Dead worms within the inflammatory tissue imply that the parasite is not well adapted for survival in this location. Presumably, *D. talismani* would elicit, and be attacked by, a similar inflammatory response irrespective of its location within the vasculature. This response was not observed in other vessels and additional work is needed to clarify the site specificity of the immune response. Our findings also suggest that cellular elements are responsible for the destruction of the larval cestodes when located in the dorsal aorta.

Effect of the Infection of the Dorsal Aorta on Natural Mortality

We found no evidence to support our original hypothesis that infected yellowfin tuna are activity limited and therefore less able to secure food. When the data from the unparasitized fish caught August-September 1985 are excluded, there are no differences in relative condition factors, relative liver weights, or relative heart weights between parasitized and unparasitized fish. When parasitized and unparasitized fish from the single school caught 15 January 1985 are compared, no significant differences in these parameters, mean short-term (i.e., RNA/DNA ratios), or mean long-term (i.e., relative otolith weights) growth are evident.

Because parasite emboli appear to cause almost complete occlusion of the anterior dorsal aorta (the only blood vessel supplying the viscera and swimming muscles), the lack of differences between infected and uninfected fish was not expected. Overstreet (1977), investigating the effects of plerocercoid infection on sciaenid fishes in the Gulf of Mexico, found no apparent detrimental effect on the host, but these parasites were found encysted in the muscle, not the vasculature. Although the ability of parasitized yellowfin tuna to function as predators are apparently not affected, their ability to escape predation remains to be tested. It is possible that infected yellowfin tuna are subjected to differential predation, as has been shown to be for roach, *Rutilus rutilus*, infected in the coelomic cavity by the plerocercoid of *Ligula* sp. (Van Dobben 1952).

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[5] Queenth, M. K. K., and R. W. Brill. 1983. Operations and procedures manual for visiting scientists at the Kewalo Research Facility. Southwest Fish. Cent. Admin. Rep. H-83-7, 16 p. Natl. Mar. Fish. Serv., NOAA, Honolulu, HI.

Pressure Flow Relationships in the Dorsal Aorta

The unphysiologically high pressures required to pump saline through the dorsal aortas of moderately and heavily infected fish remain to be explained in light of apparent lack of effects of the parasite on other measures of the fish's condition, including the absence of cardiac hypertrophy. It is possible that the dorsal aorta, because of its thick muscular wall (J. Brock, unpubl. obs.), becomes significantly less compliant postmortem. Such changes could require that higher pressures be generated to create a given degree of expansion. Therefore higher pressures would be required postmortum to push a given flow rate of saline through the vessel.

In summary, *D. talismani* appears to have no significant adverse effects on the physiological fitness and natural mortality of small yellowfin tuna in spite of apparent vascular blockage. How these fish are able to cope with dorsal aorta infection requires further investigation.

Use of *Dasyrhynchus talismani* as a Natural Tag for Tracing Movements of Small Yellowfin Tuna

We feel that this parasite offers excellent potential as a natural marker for tracking the movements of separate groups of small yellowfin tuna between or into specific fisheries. (For a review of the use of parasites to delineate stocks for management purposes, see MacKenzie 1983.) *Dasyrhynchus talismani* does not fulfill all seven requirements for an ideal natural tag listed by Sindermann (1983), but it does appear to meet the requirements of 1) having significant differences of geographic prevalence, 2) being easily detected, 3) being able to be definitively identified, 4) having minimum effect on host survival, and 5) surviving in the host for long periods. Data on prevalence of *D. talismani* could be combined with data on prevalence of other parasites, as has been shown by Lester et al. (1985) for skipjack tuna, or combined with data on relative condition factor, relative heart weight, and relative liver weight to provide information on fish movements.

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NATIONAL MARINE FISHERIES SERVICE

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INTRODUCTION

We noted in the Minerals Management Service's Environmental Study Plan for FY 1988 that additional emphasis will be placed on fisheries studies. We applaud this approach and anticipate the prospect of more frequent interchanges between our agencies. We also appreciate the opportunity to participate in this meeting and to describe some of our activities in the southwestern United States.

Fisheries and environmental databases of the National Marine Fisheries Service (NMFS) are extremely varied in structure and form: from handwritten logs to scientific publications to computer-based data sets. In this overview, we will emphasize several databases actively maintained by the National Marine Fisheries Service and other fisheries-oriented agencies on the west coast.

Our intention is to provide a brief sketch of: 1) our agency and its mission; 2) the data sets we have collected and maintained in support of our work; and 3) an opening to what we hope will be a broader discussion of our respective roles in this business of resource management. We were asked specifically to describe the California Cooperative Fisheries Investigations (CalCOFI) data collections. We will also attempt to convey a broader perspective on our involvement in the management of living marine resources in the southwestern U.S.

THE MISSION OF THE NMFS

The National Marine Fisheries Service is part of the National Oceanic and Atmospheric Administration (NOAA), under the Department of Commerce. In California and the western Pacific, we maintain four research laboratories, collectively referred to as the Southwest Fisheries Center, and four regional offices, collectively referred to as the Southwest Region. In conducting our field work, we employ two NOAA research vessels.

There are five major components to our mission, which is to provide information for the management of living marine resources. These components are:

- Manage the harvest of fish and shellfish within the 200 fishery conservation zone.
- Grant permits for the incidental take of marine mammals.
- Ensure the recovery of endangered marine species and promote the protection of marine habitats.
- Promote the development of latent fisheries resources.
- Conduct research for better methods of determining stock productivity and the impacts of regulation on both man and fish.

There are no easy recipes for achieving these objectives. In fact, there is the potential for controversy in every area in which we are involved. For this reason, the agency is organized such that the analysis of problems (the realm of the research labs) is separate from the implementation of solutions (the realm of the regional offices).

Regional offices in the southwest are located in Terminal Island, Santa Rosa and San Diego, California and Honolulu, Hawaii. These offices access a variety of information sources in order to:

- Monitor harvests and issue regulations for managed fisheries and identified marine habitats.

- Issue permits to kill or capture marine mammals.

- Manage the fisherman's loan fund and assistance programs.

- Publish fish market news.

The regional offices are a good source of data on the fishing industry, particularly econometric information and environmental issues.

We also maintain research laboratories in La Jolla, Tiburon, Monterey and Honolulu. Their purpose is to generate information and options for the management of exploited populations. To do that, we must consider the ability of a given population to sustain harvest. We must also consider the influence of climatic events and the magnitude of natural variability of population size. Within the laboratories, the research is organized into four major areas:

- Coastal fish populations.
- Marine mammals, both coastal and high seas.
- Large pelagic fishes, tuna and billfishes.
- Insular fish populations.

Many of our data collections are conducted to answer specific research questions. Others, however, are attempts at large-scale integrations of physical and biological processes over extended time periods; one of these is the CalCOFI program.

DATA COLLECTION

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) was established in response to concern over the decline in California sardine landings. Landings dropped from 600,000 tons annually in the 1930s and 1940s to 100,000 tons in 1949, landings virtually disappeared in the early 1950s. At that time, the major unknown was the relative influence of man and the environment on the sardine population. Eventually it was concluded that overfishing changed the demography of the sardine population and reduced its ability to weather environmental regimes which were adverse to good recruitment.

CalCOFI is a consortium of three marine research agencies, all operating in California. These agencies and their contributions to CalCOFI are:

- California Department of Fish and Game (CDF&G), which monitors the catches of adult fish and conducts juvenile fish surveys.

- Scripps Institution of Oceanography (SIO), which describes the physical environment and monitors phytoplankton and zooplankton distribution and abundance.

- National Marine Fisheries Service (NMFS), which describes the production of pelagic fish eggs and larvae.

Each of these agencies has a unique history and charter. It is remarkable that in 1949, they were able to agree that an understanding of the large-scale processes at work in the California Current was essential to their respective objectives; that such an undertaking would require their combined resources in a cooperative effort; and that this was the only way to avoid another tragedy like the sudden decline of the sardine population. This cooperation has lasted for four decades.

Thus, the reproduction, early survival, growth, recruitment, and harvest of fish populations were, and continue to be, described in relation to their biological and physical environments. This became known as the "oceanographic approach" to fisheries research. CalCOFI cruises were conducted monthly from 1949 through 1960, then quarterly through 1966, and again monthly every three years through 1981. In recent years, cruises have been conducted on a quarterly basis. There have been over 300 cruises since 1949.

Output from the CalCOFI program includes:

- Data Reports. Thirty-five data reports have been published by CDF&G describing the results of their trawl surveys for juvenile fish. Over 300 data reports have been published by SIO describing the physical, chemical and biological data collected on CalCOFI survey cruises; these reports are now published within three months of the completion of a cruise. The data include measurements of various nutrients, plant pigment, phytoplankton and zooplankton biomass, salinity, temperature, water clarity, and several other observed as well as derived variables. These data, as well as NMFS collections of fish eggs, and larvae, are also available in a digitized format.

- Atlases. Thirty atlases have been published under the CalCOFI name. These atlases graphically depict many of the data sets in a standard format. Topics range from geostrophic flow to primary production to flatfish larvae.

- CalCOFI Reports. Twenty-seven volumes of CalCOFI reports, containing over 700 peer-reviewed publications, have been published to date. This regional journal has gained a worldwide readership due to the quality of submissions and the global interest in eastern boundary currents as centers of intense and highly variable biological productivity.

The first multidisciplinary symposium on the El Niño phenomenon was sponsored and published by CalCOFI after the intense warm period of 1957-58. Other symposia have examined the facts and fallacies of fishery science, nearshore processes, large-scale aperiodic fluctuations, climatic regimes and trends, sea birds and pinnipeds, and numerous other topics.

In addition to CalCOFI, other databases concerning fisheries and marine mammal populations off the west coast include:

Aerial Surveys: Sightings of fish schools by observer aircraft employed in the purse seine fishery off southern California have been maintained from 1963 to the present. Data include location, species, and an estimate of school weight. Species included in this database are sardine, anchovy, squid, bonita, jack mackerel, Pacific mackerel, and several tuna species.

Albacore: Extensive data sets and analyses are maintained on this species and its fishery. These include: 1) detailed data on the fishery from fishermen log books; 2) migration patterns derived from extensive tagging data; and 3) estimates of population levels and fluctuations prepared by both Japanese and American fisheries agencies.

Coastal Reef Ecosystem: Two sites, one in southern California and one in northern California, have been monitored for over 12 years. Observed changes in the structure of fish, invertebrate and plant communities have been correlated with large-scale climatic regimes. Data are collected by divers and are used to elucidate species diversity, planktonic and benthic communities, and predator-prey relationships. All specimens of plants and animals are identified to species; more than 20 new species of invertebrates have been described from this study.

Rockfishes: Since 1984, several species of rockfish have been collected at sites in the Gulf of the Farallons and in Monterey Bay. The data describe population fluctuations based on juvenile abundances, age and growth curves, parasite burdens, diseases, and fecundity.

Fish Landings: The Fishery Information Network (FIN) is a database established cooperatively by west coast states and NMFS to support the management of coastal fisheries. States provide weekly summaries of commercial fish catches to the Pacific Marine Fisheries Commission, who are under contract to the Council to maintain the database.

Coastal Marine Mammals: Over the last several years, considerable information has been collected on the life history, food habits, and population trends of California seal lions, elephant seals, harbor seals, and harbor porpoises.

Other data include several time series of climatic indicators generated by our laboratory in Monterey, and a five-year survey of the living marine resources of the northwest Hawaiian archipelago conducted by the NMFS laboratory in Honolulu in cooperation with the State of Hawaii and the Fish and Wildlife Service.

RESOURCE MANAGEMENT ISSUES

We believe that the research goals of our two agencies are very similar in regards to living marine resources, which are to:

- Determine the impact of exploitation on the abundance and production of biological populations.

We must start with an understanding of these impacts before we can begin to formulate management options. Such an understanding requires knowledge of resident populations, their relationship with predator and prey populations, and their relationship to the physical environment. Obviously, such things cannot be known with certainty and the risks associated with various management options must also be evaluated. Risk analysis requires knowledge of the natural variability of populations and the causes of this variability.

To gain this knowledge, NMFS conducts surveys over large spatial and temporal regimes. Data from these surveys are used to describe: 1) the distribution, reproduction and recruitment of populations; 2) the physical habitats and their seasonal change; and 3) long-term variability and trends. This information is used as a context for specific studies to determine the effects of various management options.

We believe that government agencies are appropriate for conducting this kind of long-term monitoring. They possess the facilities required including ships, labs, and reference collections; they also operate on long-term funding rather than project funding. Accordingly, MMS should fund specific studies which draw on these long-term studies as background information. Meetings like this, convened to exchange information, are required for this division of labor to work. Of equal importance is adequate funding to publish both data and analyses, which should be subject to peer review and disseminated widely.

We propose that new research efforts related to development on the Outer Continental Shelf (OCS) should concentrate on specific studies designed to answer questions regarding proposed management actions. Existing fisheries database, such as described here, are adequate to identify the geographic areas, species of fish and marine mammals, and fisheries that could be affected by development on the OCS. With few exceptions, however, the data we have described do not answer questions regarding what effects the selection of a specific option of exploitation will have on the biological populations at a given site. Unless research is designed to give definitive answers to relevant questions, and within a reasonable time frame, the work is of little value to the decision process.

QUESTIONS AND DISCUSSION

Question (Pershing): How accurate are the individual locations of animals specified in the individual databases, particularly the CalCOFI databases and the California Fish and Game databases?

Response (Carr): Individual sightings of only marine mammals?

Question (Pershing): I'm particularly interested in marine mammals. Do you actually have records for the individual sightings?

Response (Carr): In the case of marine mammals most of the work is done when they are out of the water and thus there are very specific sites in the Channel Islands. Most, or all, of the population estimates are made when they are on shore. We found it very difficult to do it any other way. We tried doing it with aerial and ship surveys for the harbor porpoise, but it was very difficult.

Question (Chamberlain): In your observations of fish schools in southern California, was there an equal effort in all areas or was there bias closer to the airport or to the coast?

Response (Carr): I would say there is a great deal of bias. The observers are looking for fish and of course they avoid areas where the fish are not. The bias is primarily in the lack of objectivity.

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Commercial Passenger Fishing Vessel Landings of Widow Rockfish *Sebastes entomelas* in Central California

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ABSTRACT

Commercial fishing for widow rockfish (*Sebastes entomelas*) has increased significantly in northern and central California since the summer of 1981. In central California, widow rockfish are also found in commercial passenger fishing vessel landings. For this reason, the importance of widow rockfish to the central California recreational partyboat fishery was investigated during a three-year study period from 1977 to 1979. Landings of widow rockfish by the recreational partyboat fishery were minor. Only 3.7% of the catch per unit of angling effort were widow rockfish. The catch of widow rockfish was greatest in northern ports and on trips taken during winter months. This rockfish may have been the target species of some winter recreational partyboat trips at San Francisco and Bodega Bay.

INTRODUCTION

Rockfish fishing by commercial passenger fishing vessels (CPFV) and commercial trawl vessels is highly developed in some areas of northern and central California. Landings of rockfish by the commercial trawl fishery have been increasing since 1977, and projections indicate that they will continue to do so (Pac. Fish. Manage. Council 1981). Increased markets as well as the ability of commercial fishermen to target on one species, widow rockfish (*Sebastes entomelas*), have contributed significantly to these landings. Concurrently, the increasing proportion of rockfish (genus *Sebastes*) in the CPFV catch is projected to be a trend in the recreational partyboat landings of central California for the next ten years (Gruen and Gruen 1979). Potential exists, therefore, for competition between the recreational partyboat and commercial trawl fisheries for the available resource. This paper presents analyses of the CPFV rockfish fishery, the relative importance of widow rockfish to this fishery, and the estimated effect upon the recreational partyboat catch in the event of a significantly reduced widow rockfish stock.

Very few data are available from the complex recreational and commercial fisheries for rockfish of central California. These fisheries are complex due to their multispecies nature, the fact that landing and catch-per-unit-effort statistics do not specify species, and sampled landings traditionally have not included age and sex composition. Because of this lack of necessary data, the Tiburon Laboratory of the National Marine Fisheries Service and the California Department of Fish and Game have been cooperating since 1977 in a program to routinely sample both recreational and commercial landings for species, sex, length, and age composition. Presented here is an analysis of the central California CPFV fishery sample data obtained during a three-year study period from 1977 to 1979. Also presented, for comparison, are expanded sample data from the central and northern California commercial trawl fishery for the same period. Because a change in the widow rockfish fishery occurred during 1981, preliminary data for that year are also reviewed.

METHODS

Sampling was concentrated on rockfishing trips around the major ports of Monterey, Half Moon Bay, San Francisco, Bodega Bay, Fort Bragg, and Eureka. There were, however, virtually no CPFV landings of rockfish north of Bodega Bay. Sampling effort averaged 290 samples per year; each sample consisted of from one to four clusters. Fish traditionally were landed whole and placed in burlap bags. The fish in a bag often were the combined catches of several anglers and there was little possibility of telling which fish were caught by a particular angler. Tomlinson's (1977) recommended sampling frame used, therefore, not the more traditional angler but the burlap bag as the sampling unit.

Catch data were obtained from interviews of a random sample of anglers for each sampled trip. A principal assumption during the interview was that the content of each bag was the catch of one angler. However, since more than one angler may contribute to one bag, estimates of catch per angler may be positively biased. Biological data, including species, sex, length, and otoliths, were collected in the field. Age determinations were made later at the Tiburon Laboratory.

Expansion of sample data to the total catch, as depicted in each table, was completed at the Tiburon Laboratory, using the Lawrence Berkeley Laboratory CDC 7600, by the method indicated below:

$$\widehat{YR} = \hat{A}\,\widehat{\overline{YR}}$$

where $\widehat{YR}$ = estimated total number of fish captured (species-sex-length-age) derived from total trips and mean number of anglers per trip.

$$\hat{A} = N\,\bar{a}$$

where $\hat{A}$ = estimated total rockfish anglers,
N = total number of rockfish trips,
$\bar{a}$ = mean number of anglers per sampled trip,

$$\widehat{\overline{YR}} = \sum_{i=1}^{n} (y_i/l_i)L_i / \sum_{i=1}^{n} A_i$$

where $\widehat{\overline{YR}}$ = mean number of fish (species-sex-length-age) captured per angler,
n = sampled trips,
A_i = anglers per trip i,
y_i = fish (species-sex-length-age) sampled per trip i,
l_i = total fish sampled per trip i,

$$L_i = \Big(\sum_{j=1}^{m_i} l_{i,j}\Big)A_i/m_i$$

where L_i = total fish captured per trip i,
$l_{i,j}$ = catch for jth bag ith trip,
m_i = number bags examined during interview (assumed equal to number of anglers interviewed) per trip i.

All variables were derived from sampled data with the exception of N which is summary information provided by California Department of Fish and Game CPFV logs. Mean catch per sample unit $\left[\Big(\sum_{j=1}^{m_i} l_{i,j}\Big)/m_i\right]$ data were insufficient to conduct within-trip expansion of the 1977 sample data. Estimates of average $l_{i,j}$ from 1978 and 1979 were substituted, therefore, to provide total fish number expansion values presented in Tables 1 and 2.

RESULTS AND DISCUSSION

Species composition

The estimated number of rockfish landed by the CPFV and commercial trawl fisheries during 1977-79 in northern and central California ports totaled 13,310,187. Rockfish landings from CPFV accounted for 30.5% of this total (Table 1). An estimated 244,511 widow rockfish also were landed by both gear types, of which the CPFV fishery contributed 50.7%. There was no evidence, at the time of this study, of a clear gear-type dominance in the number of widow rockfish landed. Subsequent to this study, a large expansion of the northern and central California commercial trawl fishery occurred. During 1981, the first year of the expanded fishery, the annual number of widow rockfish landed by the commercial trawl fishery increased by a factor of 35. Preliminary data do not indicate that there was a comparable expansion of the CPFV fishery. Thus the relative importance of the partyboat fishery in landings of all rockfish and widow rockfish probably has declined since 1979.

The CPFV fishery landed more rockfish in the second and third quarters than during the other quarters (Table 2). Both the number of trips and anglers were also higher during the two middle quarters (Table 3). However, when compared to the two middle quarters, fishing success was considerably higher for widow rockfish and all rockfish combined during the first and fourth quarter (Table 3). Thus the relatively high landing of fish during the middle quarters was due to high fishing effort, not high fishing success.

While the largest percentage of rockfish partyboat trips, rockfish anglers (Table 5), and all rockfish landed by the CPFV fishery (Table 4) occurred in the port of Monterey, the largest contribution by widow rockfish to the catch-per-unit of sampling effort was made in the northern ports of San Francisco and Bodega Bay (Table 5). Widow rockfish contributed 4 percent to this annual catch and 7 percent during the first and fourth quarter in the northern ports. When widow rockfish did appear in the catch of trips taken from the northern ports, they appeared in relatively large concentrations. The mean percent of widows in the catch-per-bag, for those trips with any widows in the catch, was 19% for the first and fourth quarter. Furthermore, when all trips are considered, widow rockfish were important to the success of certain trips taken during the first and fourth quarter and from the northern ports of San Francisco and Bodega Bay. During the last quarter of the year, the catch for over 12% of the trips was more than 25% widow rockfish, and in 5 percent of the trips widow rockfish comprised at least 45% of the total catch.

Age composition

A comparison of data between sample years 1978 and 1979 indicates a noticeable increase in landings of younger widow rockfish (Fig. 1). An estimated 26% of the widow rockfish landed during 1978 were less than 9 years old, and 7 percent were 4 years and younger. In 1979, landings of widow rockfish less than 9 years old increased to 53%, and those less than 4 years increased to 22%. Widow rockfish first became vulnerable to the CPFV fishery at the age of 4 and 2 years during 1978 and 1979, respectively.

Full recruitment is traditionally defined as that point in the catch curve closest to the modal age (Ricker 1975). The first ages at which recruitment could be considered complete for widow rockfish captured by the CPFV fishery were 10 years-old in 1978 and 4 or 5 years-old in 1979. By comparison, the northern and central California commercial fishery during the same sampling period typically had modal ages for widow rockfish of 9 and 10 (W. H. Lenarz, Tiburon Lab., Natl. Mar. Fish. Serv., NOAA, Tiburon, CA, pers. commun.). Therefore, it appears widow rockfish may be fully recruited to the recreational partyboat fishery 5 years earlier than to the commercial fishery during periods of influx by a strong year-class. Other than during such times, the data indicate that both fisheries tend to rely upon the same year-classes.

Table 1—Comparison of the estimated number of all rockfish and widow rockfish, *Sebastes entomelas*, landed by the commercial passenger fishing vessel (CPFV) and commercial trawler rockfish fisheries at Monterey, Half Moon Bay, San Francisco, and Bodega Bay, CA.

	CPFV		Commercial trawler	
Year	All rockfish	Widow rockfish	All rockfish	Widow rockfish
1977	1.488.939	67.796	2.574.463	9.817
1978	1.269.921	20.506	2.519.546	39.673
1979	1.298.904	35.764	4.158.414	70.955
1981[1]			5.487.582	1.403.020

[1] First year of widow rockfish fishery expansion into study area.

Table 2—Quarterly landings at Monterey, Half Moon Bay, San Francisco, and Bodega Bay, CA, of widow rockfish, *Sebastes entomelas*, and all rockfish, by the commercial passenger fishing vessel (CPFV) and commercial trawler rockfish fisheries, 1977-79 and 1981.

	CPFV 1977-79	
Quarter	All rockfish	Widow rockfish
1	177.280	6.228
2	340.547	5.820
3	517.936	9.262
4	248.651	6.826

	Commercial trawler			
	1977-79		1981	
	All rockfish	Widow rockfish	All rockfish	Widow rockfish
1	655.738	35.086	834.094	98.604
2	946.250	1.356	866.825	8.572
3	752.484	18.366	1.426.128	122.832
4	984.510	507	2.360.535	1.173.012

Table 3—Estimates derived from expanded sample data of fishing effort by quarter for commercial passenger fishing vessels (CPFV) at Monterey, Half Moon Bay, San Francisco, and Bodega Bay, CA, 1977-79.

	Percent		Catch per bag	
Quarter	Boat trips	Angler days	All rockfish	Widow rockfish
1	14.9	14.7	15.0	0.52
2	27.0	26.1	11.5	0.23
3	35.7	39.7	12.2	0.30
4	22.5	19.6	13.7	0.89

Table 4—Estimates derived from expanded sample data of percentage of all rockfish and widow rockfish landed in N. Calif. by area, commercial passenger fishing vessel (CPFV), and commercial trawler rockfish fisheries.

	CPFV 1977-79	
Port	All rockfish	Widow rockfish
Monterey	43.3	20.9
Half Moon Bay	23.7	14.5
San Francisco and Bodega Bay	32.7	64.6

	Commercial trawler			
	1977-79		1981	
	All rockfish	Widow rockfish	All rockfish	Widow rockfish
Monterey	55.3	45.8	31.4	9.9
Half Moon Bay	2.5	2.2	0.2	0.1
San Francisco and Bodega Bay	42.2	52.0	68.4	90.0

Table 5—Estimates derived from expanded sample data of fishing effort by area for commercial passenger fishing vessel rockfish fishery during 1978 and 1979.

	Percent		Catch per bag	
Area	Boat trips	Angler days	All rockfish	Widow rockfish
Monterey	44.0	48.6	13.9	0.1
Half Moon Bay	30.6	24.4	11.2	0.4
San Francisco and Bodega Bay	25.4	27.0	14.4	0.7

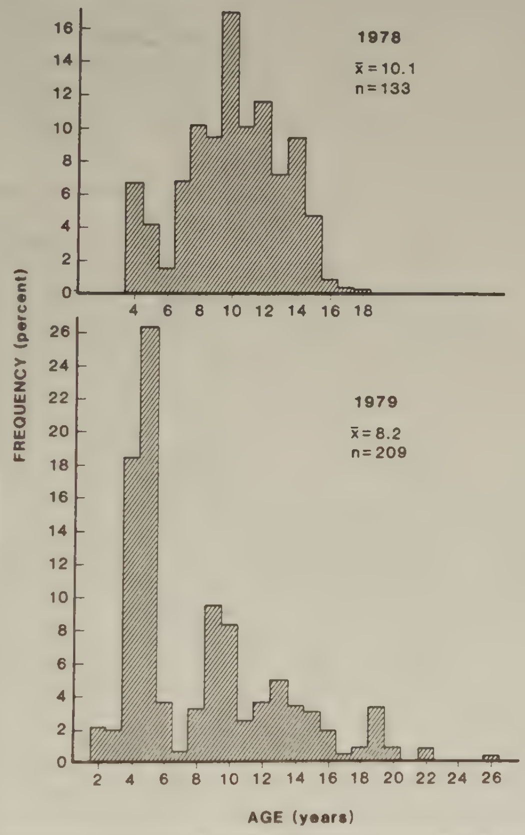

Figure 1—Age composition of widow rockfish, *Sebastes entomelas*, from 1978 and 1979 commercial passenger fishing vessel samples expanded to total landings for Monterey, Half Moon Bay, San Francisco, and Bodega Bay. Mean age ($\bar{x}$) and number of specimens sampled (n) indicated.

CONCLUSION

Widow rockfish is not an important species in the total landings of the CPFV rockfish fishery in central California. A depletion of widow rockfish stocks would decrease the annual catch of a CPFV angler by less than one-half a fish. Widow rockfish stock depletion would, however, noticeably reduce the CPFV catch in the northern ports, especially during the fourth quarter. The high percentage of widow rockfish landed on some trips taken out of Bodega Bay and San Francisco during the last quarter suggests fishermen were targeting on widow rockfish. A reduction in widow rockfish availability may then necessitate a change in CPFV fishing tactics in northern ports during portions of a year.

The results of this study suggest that monitoring the CPFV fishery age-catch data would be useful in indicating the presence of a strong year-class of widow rockfish 4-5 years prior to its full recruitment by the commercial trawl fishery. They would provide evidence for projections of widow stock strength or weakness.

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Isolation and Characterization of a New Zinc-Binding Protein from Albacore Tuna Plasma[†]

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ABSTRACT: The protein responsible for sequestering high levels of zinc in the plasma of the albacore tuna (*Thunnus alalunga*) has been isolated by sequential chromatography. The glycoprotein has a molecular weight of 66 000. Approximately 8.2% of its amino acid residues are histidines. Equilibrium dialysis experiments show it to bind 3 mol of zinc/mol of protein. The stoichiometric constant for the association of zinc with a binding site containing three histidines was determined to be $10^{9.4}$. This protein is different from albumin and represents a previously uncharacterized zinc transport protein.

High levels of zinc, relative to other trace elements, in the tissue of fish have been recognized for a long time (Vinogradov, 1953). Plasma of the albacore tuna (*Thunnus alalunga*), for example, has a zinc level more than 12 times higher than human serum. It is clear from the work of many investigators [see Vallee (1959)] that in biological systems zinc must exist as complexes with organic ligands rather than as free ions in solution. This paper presents our isolation and investigation of the plasma protein in albacore which is responsible for complexing the large amount of endogenous zinc. Fletcher and Fletcher (1978) described a similar Zn-binding protein(s) in winter flounder responsible for binding almost all plasma zinc.

Since zinc in plasma is chelated to endogenous ligands, only high-affinity sites on a plasma-binding protein are likely to be occupied under biological conditions. We have therefore designed experiments to characterize such sites by chelating the zinc with a well-characterized ligand in order to prevent hydrolysis and to form a mathematical basis with which to quantitate the competition for protein uptake of this metal. Experiments using competitive chelation to modulate zinc binding to proteins have been carried out with some enzymes (Cohen & Wilson, 1966; Billo et al., 1978). We have generalized this approach to multicomponent zinc-binding systems and have adapted the traditional Scatchard analysis of equilibrium binding to investigate the high-affinity Zn-binding sites on the tuna protein.

MATERIALS AND METHODS

Albacore Plasma. Albacore were captured with hook-and-line in the Pacific Ocean within 200 miles of San Diego during the months of July and August of 1979–1983 aboard the N.O.A.A. research vessel *David Starr Jordan*. Blood was collected immediately in syringes by cardiac puncture. Because blood clotting and clot dissolution occur almost simultaneously in this fish, true "serum" was not obtained; rather, plasma was collected within 30 min of bleeding after centrifugation of red cells at approximately 2000*g* for 15 min at room temperature. Plasma was stored frozen at −18 °C.

Radiozinc Solutions. $^{65}ZnCl_2$ ("carrier-free"; New England Nuclear Corp., Boston, MA; specific activity 6–7 mCi/mg) was diluted into 0.1 N HCl prior to use. Radioactivity measurements were made in a Nuclear-Chicago Model 1085 γ well counter with the spectrometer calibrated to capture the 1.11-MeV emission (±10%) of ^{65}Zn.

Protein Purification. (*A*) *Rationale for Purification.* At the beginning of our studies, we were able only to distinguish the tuna plasma Zn-binding protein as one of the two most anodal "albumin-like" bands in sodium dodecyl sulfate (SDS) gel electrophoresis (data not shown). For purification, we therefore explored chromatographic systems that would fractionate these two bands, which seemed similar in size and electrophoretic mobility, on the basis of properties other than charge alone. Metal-chelating resins with iminodiacetate functionalities have been used successfully for affinity chromatography of other metal-binding proteins (Muszynska et al., 1986). Lectin affinity chromatography has been of value in the separation of various non-glycoprotein plasma albumins

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(Hrkal & Vodrazka, 1977; Aspberg & Porath, 1970). After performing numerous development studies, we adopted a three-step chromatographic procedure that yielded a purified fraction showing a single band on SDS gel electrophoresis.

The Zn-binding protein of plasma was purified as described below by sequential chromatography on (a) Sepharose 6B (Pharmacia) reduced with borohydride according to Lonnerdal and Hoffman (1981), (b) chelating Sepharose 6B, and (c) concanavalin A–Sepharose 4B. All columns were run at room temperature. In order to facilitate tracing of the Zn-binding components, plasma was labeled with $^{65}ZnCl_2$ by adding a small quantity of "carrier-free" $^{65}ZnCl_2$ to give approximately 6×10^4 cpm/mL of plasma.

(*B*) *Gel Filtration Chromatography*. One milliliter of labeled plasma was dialyzed against equilibration buffer [0.01 M *N*-(2-hydroxyethyl)piperazine-*N'*-2-ethanesulfonic acid (HEPES), 1.0 M NaCl, and 0.02% phenylmethanesulfonyl fluoride (PMSF), pH 7.0] and applied to a 1.5 × 51.5 cm column of Sepharose 6B. The radioactive peak was pooled. Figure 1 shows a typical elution profile.

(*C*) *Zinc Affinity Chromatography*. A column of chelating Sepharose 6B (1.0 × 28.5 cm) was prepared by applying 50 mL of 22 mM $ZnSO_4$ to saturate the iminodiacetic acid residues. The column was subsequently washed with equilibration buffer (0.01 M HEPES, 1.0 M NaCl, and 0.02% PMSF, pH 7.0) to remove unbound zinc. The pooled radioactive protein peak from the preceding step was then applied. The column was rinsed with 1 column volume of buffer to remove unbound protein. Bound protein was removed with a linear gradient of decreasing pH formed by continuous mixing (Hegenauer et al., 1965) of 30 mL of 0.01 M sodium acetate (NaOAc) and 0.02% PMSF, pH 5.0, with 30 mL of 0.01 M NaOAc and 0.02% PMSF, pH 2.0 (HCl). Figure 2 shows a typical elution profile. Radioactive zinc was lost from the protein in the pH gradient; therefore, all protein peaks were checked for zinc uptake by using equilibrium dialysis in order to identify the zinc-binding peak(s). Zn binding was found only in the last peak from the gradient. The last protein peak was eluted at pH 3.0 during protonation of the iminodiacetic acid residues, causing ionic zinc to be released into solution. The protein peak was pooled, but before the protein solution was neutralized, excess ionic zinc was removed by repeated ultrafiltration through an Amicon Model 8010 stirred ultrafiltration cell (10000 molecular weight cutoff membrane) using pH 3.0 NaOAc washes. The pH was increased to 7.0 by dialysis against the subsequent column buffer.

(*D*) *Lectin Affinity Chromatography*. The Zn-binding peak was then applied to concanavalin A–Sepharose 4B (1 × 17 cm). Approximately 2 column volumes of equilibration buffer (0.02 M NaH_2PO_4, 1.0 M NaCl, and 0.02% PMSF, pH 7.0) were applied to remove all unbound proteins. Bound proteins were eluted with 0.5 M methyl mannoside dissolved in equilibration buffer. One-half column volume of elution buffer was applied to the column and then allowed to stand and equilibrate for 30 min. Elution was continued for approximately 2 column volumes. The column was then washed with the starting buffer, and protein peaks were collected. Figure 3 shows a typical elution profile.

(*E*) *Removal of Metal*. Several batches of protein were purified as described above, checked for electrophoretic purity, and pooled. The protein was rendered zinc free by adjusting the pH to 3.0 with HCl and repeatedly washing it on an ultrafiltration membrane with 10-mL portions of 10 mM sodium acetate/HCl, pH 3.0, until the ultrafiltrate contained less than 50 nM zinc. Stock protein solution was finally equilibrated by dialysis with the same buffer and electrolyte system used in subsequent experiments. The zinc content of this protein solution was determined by graphite furnace atomic absorption spectrophotometry to be 34 nM. This "background" level of zinc had no significant effect on our results. Protein concentration was determined by the method of Lowry et al. (1951) using a bovine serum albumin standard.

Electrophoresis. Electrophoresis was carried out in an 8% polyacrylamide slab gel prepared with final concentrations of 0.375 M tris(hydroxymethyl)aminomethane hydrochloride (Tris-HCl)/0.1% sodium dodecyl sulfate (SDS), pH 8.8, with a 3% stacking gel. The ratio of acrylamide:bis(acrylamide) was 29.1:0.9. Ten microliters of *N,N,N',N'*-tetramethylethylenediamine (TEMED) per 20-mL total volume and 0.03% ammonium persulfate were used to catalyze polymerization. Running buffer was 0.025 M Tris–glycine/0.4% SDS, pH 8.9. All gels were run at 45-mA constant current for approximately 2.5 h, using the gel apparatus described by Studier (1973). Bio-Rad SDS–polyacrylamide gel electrophoresis (PAGE) low molecular weight standards were used as markers. Gels were stained by using the Kodavue electrophoresis visualization kit (Eastman Kodak). The concentration of applied protein was determined by the method of Lowry et al. (1951).

Amino Acid Analysis. Protein was hydrolyzed in 6 N HCl for 24 h at 110 °C in sealed evacuated tubes. Analysis was performed by using a Beckman 118C analyzer.

Zinc Chelates. Stock solutions of reagent-grade $ZnSO_4 \cdot 6H_2O$, HEPES, NaCl, and disodium nitrilotriacetate (NTA) were prepared in quartz-distilled water. In preparation of the radiozinc chelate for dialysis experiments, $^{65}ZnCl_2$ was equilibrated with zinc sulfate for 15 min; the total zinc concentration from $^{65.38}Zn$ plus ^{65}Zn was calculated by reference to radiochemical specifications before addition of NTA. The NTA:Zn molar ratio was 1.1:1. The final specific activity of the zinc chelate was 0.348 mCi/mg. Radiozinc was at most 5% of the total zinc. HEPES and NaCl were added to final concentrations of 0.03 and 0.25 M, respectively. A small amount of dilute 0.01 N NaOH was added to achieve the final pH before diluting to volume. Ligand concentration was calculated from the concentration of stock solutions.

Equilibrium Dialysis. Experiments were performed in plastic cell compartments separated by a single thickness of no. 20 Visking tubing (Union Carbide Corp.) as described by Malmstrom (1953); the interior of the cells was coated lightly with silicone grease to prevent adsorption of zinc to the acrylic surface. One milliliter of protein solution and 1.0 mL of radiozinc chelate were pipetted on opposite sides of the membrane. Filling holes were sealed with tape, and cells were agitated on a reciprocal shaker (~1 excursion/sc) for 3 days at 4 ± 0.5 °C. Samples (850 μL) were withdrawn from each cell compartment for measurement of ^{65}Zn. The proportion of protein-bound metal in each cell was calculated from the relationship (^{65}Zn in retentate − ^{65}Zn in diffusate)/(^{65}Zn in retentate + ^{65}Zn in diffusate). We observed no change in the relative volumes of the protein and chelator compartments during dialysis. The final pH was measured at 22 °C with a Radiometer GK2302C ceramic junction combination electrode.

Metal–Ligand Equilibria and Calculations of Ionic Zn. Standard equilibrium equations and equations for computing the concentration of Zn^{2+} ion have been derived and are available on request.

Scatchard Analysis. Traditional Scatchard analysis plots the relationship between the ratio of protein-bound metal to

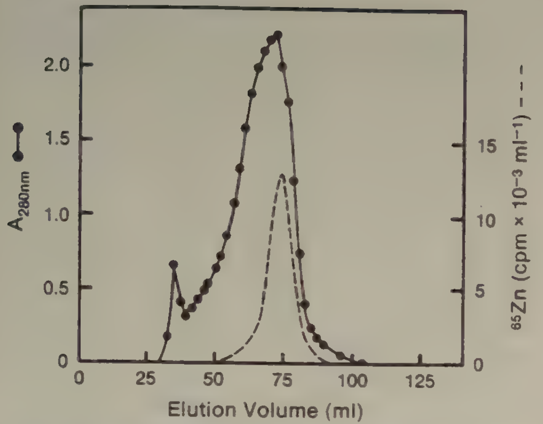

FIGURE 1: Typical elution profile of ^{65}Zn-labeled albacore blood plasma on Sepharose 6B-200 reduced. HEPES/NaCl buffer, pH 7.0.

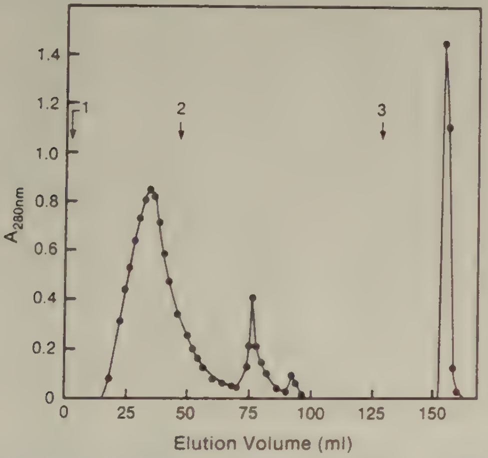

FIGURE 2: Typical elution profile of pooled radioactive peak from Sepharose 6B-200 (Figure 1) on chelating Sepharose 6B (Zn^{2+} form). Arrows: 1, sample loaded and column washed; 2, pH gradient begins; 3, column wash begins.

free metal vs. protein-bound metal. For this treatment, "free" metal is considered to be the difference between metal presented and metal bound to protein (Scatchard, 1949). Siiteri (1984) points out that, in binding studies, the appropriate value for the "free" component (in our case, zinc) is the active species which is not bound to any other moiety in the system. In our experiments, zinc has been presented to the protein in the form of its NTA chelate. This reduces the availability of the zinc for binding except to sites with an affinity greater than NTA. According to Siiteri's suggestion, the values used for "free" zinc in our Scatchard plots are those obtained by calculating ionic zinc (Zn^{2+}) only.

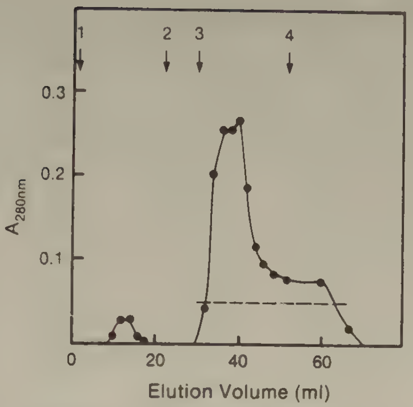

FIGURE 3: Typical elution profile of Zn peak from chelating Sepharose 6B (Figure 2) on concanavalin A–Sepharose 4B in phosphate/NaCl buffer, pH 7.0. Arrows: 1, sample loaded and column washed; 2, methyl mannoside loaded and equilibrated for 30 min with column; 3, column eluted with methyl mannoside; 4, column wash begins.

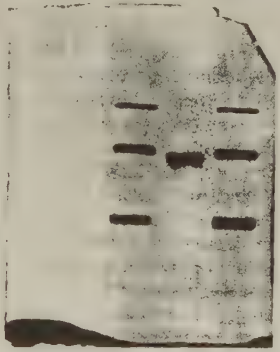

FIGURE 4: Acrylamide gel electrophoresis of Zn protein and comparison with molecular weight markers. Lanes 1 and 3 show phosphorylase *b* (M_r 92 500), bovine serum albumin (M_r 66 200), ovalbumin (M_r 45 000), carbonic anhydrase (M_r 31 000), and soybean trypsin inhibitor (M_r 21 500). Lane 2 shows the Zn protein estimated to be M_r 66 000.

Table I: Purification Table

method	total volume (mL)	total protein (mg)	zinc bound (μg)	zinc bound (μg/mg of protein)
plasma	1	93.30	44.34	0.48
gel filtration	18	59.76	43.32	0.73
Zn affinity chromatography	5	13.30	22.02	1.66
lectin affinity chromatography	5	2.05	6.70	3.27

RESULTS

Protein Purification. Figures 1–3 show typical elution profiles for the sequential purification of the Zn protein from albacore plasma on Sepharose 6B, chelating Sepharose 6B, and concanavalin A–Sepharose 4B, respectively. Metal-binding protein peaks were identified by electrophoresis and by retention of ^{65}Zn. Table I shows the progress of purification attained at each chromatographic step. On the basis of "specific activity", a 7-fold enrichment for this protein was achieved over its original concentration in tuna plasma. Two milligrams of purified protein was recovered from 1 mL of plasma (Table I). This yield represents about 15% of the total Zn-binding capacity of plasma. We therefore estimate this protein to be 14% of the total plasma proteins, so that a 7-fold enrichment represents close to the maximum possible purification. The purity of the final protein peak was greater than 95% as judged by Kodavue staining after electrophoresis and integration of stainable bands (Figure 4) by scanning densitometry. We have made progress in sequencing approximately 30 N-terminal amino acids of the tuna plasma Zn-binding protein. It is more appropriate to present these data elsewhere in more complete form. However, only a single amino acid

Table II: Amino Acid Composition of Zinc-Binding Protein

amino acid	mol %	residues/mol[a]
Asp	10.64	62
Thr	5.15	30
Ser	6.33	37
Glu	9.36	55
Pro	3.13	18
Gly	7.56	44
Ala	7.06	41
Val	6.86	40
Met	2.99	17
Ile	4.43	26
Leu	6.72	39
Tyr	4.92	29
Phe	7.05	41
His	8.15	48
Lys	6.93	41
Arg	2.52	15
Cys[b]	0.20	1
Trp	nd[c]	
	100.00[d]	584[d]

[a] Calculated by multiplying mole percent by 584 residues (66000 g/113 g per residue). [b] Cysteines were not protected. [c] nd = not determined. [d] Total.

signal has been observed at each degradation cycle. This result is strong evidence for homogeneity of this protein, since no contaminating N-terminal amino acids were detected. Molecular weight was estimated by the electrophoretic method of Weber and Osborn (1969) by reference to the R_f of molecular weight standards (Figure 4). The molecular weight of the Zn-binding protein was estimated to be 66 000.

Amino Acid Analysis. Table II shows the amino acid content of the Zn protein. Because cysteine was not protected, its value may be in error. The number of residues was calculated by dividing the average molecular weight of amino acids into the molecular weight of the protein. The value used as the average molecular weight per residue (113) was calculated by multiplying the mole percent contributed by each amino acid by its molecular weight, summing the products, and subtracting for the loss of one molecule of water. The total number of residues was then multiplied by the mole percent of each amino acid to give the number of residues per mole.

Stoichiometry Determined by Scatchard Plots. Primary data are given in Table III for binding experiments conducted in three pH ranges: 5.0, 7.0, and 8.5. Preliminary analysis of the binding data at pH 7.0 and 8.5 (Table III) confirmed the suggestion of Siiteri (1984) that the "free" (i.e., ionic and uncomplexed) zinc was the species involved in the metal-binding activity of this protein. For example, Scatchard plots of the ratio of moles of Zn:moles of protein ($\bar{v}$) vs. $\bar{v}$/[Zn] were much more linear when the zinc term was Zn^{2+} rather than total zinc not bound to protein. Figures 5 and 6 show the Scatchard plots of pH 7.0 and 8.5 data presented in this way. Visual inspection of these plots suggests that the binding increased linearly with increasing Zn^{2+} concentration to a maximum, after which binding plateaued. For each pH experiment (7.0 and 8.5), we accordingly grouped data points into two classes by a process of maximizing the correlation coefficient for two independent data sets. The correlation coefficient for the data yielding line A at pH 7.0 is –0.892; that for the data yielding line B is 0.780. The lines intersect at $\bar{v}$ = 3.26. At pH 8.5, the correlation coefficient for line A is –0.971; that for line B is 0.581. The lines intersect at $\bar{v}$ = 2.85. Data from the pH 5.0 experiment did not fit a Scatchard plot because the slope of the line was positive. Notice the clustering of data points around $\bar{v}$ = 3 where the "specific" Zn-binding sites appear to be saturated. There are two reasons for the scatter of points around $\bar{v}$ = 3. First, the protein has reached saturation, thereby preventing any real change in $\bar{v}$. Second, the experimental error increases at the higher zinc concentrations used. When zinc concentrations are low, the majority of the metal is found on the retentate side of the membrane, and the experimental error in subtracting a small number from a large number is small. However, at high zinc concentrations, the difference in zinc concentration between the two sides of the membrane is small, and the experimental error in subtracting two large numbers is correspondingly large. Therefore, the fluctuation in $\bar{v}$ at saturation is more representative of the experimental error than of a real change in $\bar{v}$. Circled points (outliers) were eliminated from regression analysis because they fell outside the 95% confidence interval of the regression line. The data at pH 7.0 were also plotted (not shown) with $\bar{v}$ vs. $[Zn]_t$ and show an asymptote at $\bar{v} \simeq 3$. These data clearly show the protein binds 3 equiv of zinc.

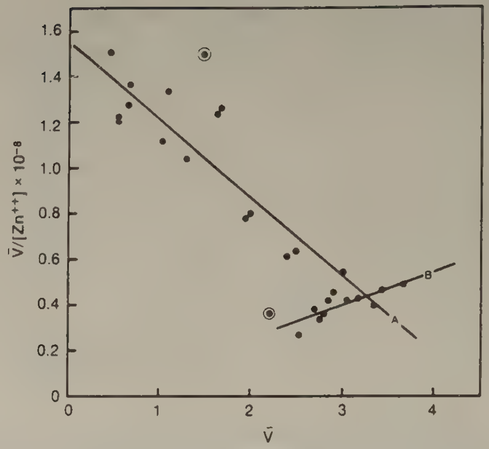

FIGURE 5: Scatchard plot of experimental data from equilibrium dialysis experiments at pH 7.0. Circled points (outliers) were eliminated from regression analysis.

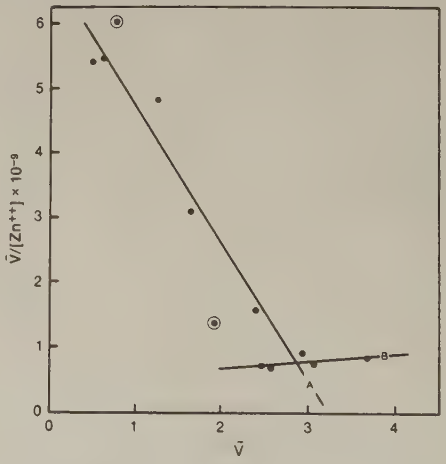

FIGURE 6: Scatchard plot of experimental data from equilibrium dialysis experiments at pH 8.5.

Strength of Zinc Binding to Protein. Primary data for equilibrium dialysis experiments with Zn-binding protein are found in Table III. We were unable to calculate equilibrium constants for values of $\bar{v} \geq 3$, i.e., at saturation. When

Table III: Primary Data and Stoichiometric Equilibrium Constant for the Binding of Zinc to Albacore Serum Protein with NTA as the Competing Ligand

equilibrium concentration (M × 10^6)								log K[a]	
NTA	total protein	protein-bound zinc	diffusible zinc	total zinc:protein ratio	$\bar{\nu}$	pH	−log free (ionic) zinc	two histidines	three histidines
1.0320	1.5625	0.051	0.8865	0.6	0.0323	5.02	6.27	7.83	9.58
1.7203	1.5625	0.031	1.5320	1.0	0.0195	4.99	6.09	7.49	9.27
3.4406	1.5625	0.023	3.1020	2.0	0.0166	4.99	5.89	7.16	8.94
5.1609	1.5625	0.082	4.6060	3.0	0.0527	4.99	5.80	7.63	9.41
6.8812	1.5625	0.210	6.0400	4.0	0.1341	4.99	5.74	8.00	9.79
13.7625	1.5625	0.393	12.1070	8.0	0.2515	4.99	5.58	8.13	9.92
27.5250	1.5625	0.200	24.8000	16.0	0.1277	4.99	5.42	7.66	9.45
55.0500	1.5625	0.226	49.7740	32.0	0.1449	4.99	5.30	7.58	9.37
82.5750	1.5625	0.818	74.1820	48.0	0.5234	4.99	5.25	8.15	9.94
110.1000	1.5625	0.369	99.6310	64.0	0.2361	5.00	5.20	7.69	9.47
137.6250	1.5625	0.668	124.3320	80.0	0.4277	4.97	5.16	7.99	9.80
165.1500	1.5625	0.408	149.5920	96.0	0.2614	5.00	5.15	7.69	9.47
192.6750	1.5625	1.057	173.9430	112.0	0.6763	4.99	5.13	8.17	9.96
220.2000	1.5625	1.196	198.8040	128.0	0.7655	5.00	5.12	8.23	10.01
1.0320	1.5625	0.740	0.1975	0.6	0.4736	6.96	8.54	8.36	8.52
1.3762	1.5625	0.865	0.3850	0.8	0.5536	6.97	8.34	8.27	8.45
1.7203	1.5625	1.033	0.5300	1.0	0.6607	6.98	8.29	8.31	8.48
3.4401	1.5625	1.727	1.3980	2.0	1.1052	6.97	8.08	8.44	8.62
5.1609	1.5625	2.328	2.3600	3.0	1.4900	6.98	8.00	8.57	8.75
6.8812	1.5625	2.625	3.6250	4.0	1.6801	6.97	7.88	8.56	8.74
13.7625	1.5625	3.121	9.3790	8.0	1.9973	6.98	7.60	8.47	8.65
27.5250	1.5625	3.893	21.1070	16.0	2.4915	6.97	7.40	8.68	8.86
55.0500	1.5625	4.688	45.3120	32.0	3.0005	6.97	7.25		
82.5750	1.5625	4.439	70.5610	48.0	2.8409	6.99	7.17	8.98	9.15
110.1000	1.562	5.370	94.6300	64.0	3.4370	6.97	7.13		
137.6250	1.5625	4.319	120.6810	80.0	2.7640	6.98	7.08	8.72	8.89
165.1500	1.5625	5.224	144.7760	96.0	3.3432	6.97	7.07		
192.6750	1.5625	3.975	171.0250	112.0	2.5442	6.97	7.02	8.35	8.53
220.2000	1.5625	8.070	191.9300	128.0	5.1691	6.97	7.08		
1.0320	1.5625	0.721	0.2167	0.6	0.4613	6.98	8.51	8.34	8.52
1.3762	1.5625	0.863	0.3875	0.8	0.5520	6.98	8.34	8.27	8.44
1.7203	1.5625	1.050	0.5130	1.0	0.6720	6.98	8.31	8.34	8.51
3.4406	1.5625	1.627	1.4980	2.0	1.0413	6.98	8.05	8.34	8.52
5.1609	1.5625	2.027	2.6610	3.0	1.2973	6.98	7.91	8.36	8.53
6.8812	1.5625	2.577	3.6734	4.0	1.6491	6.98	7.87	8.53	8.70
13.7625	1.5625	3.049	9.4510	8.0	1.9511	6.99	7.60	8.43	8.60
27.5250	1.5625	3.715	27.2853	16.0	2.3774	6.99	7.40	8.55	8.72
55.0500	1.5625	3.455	46.5450	32.0	2.2113	7.00	7.21	8.21	8.37
82.5750	1.5625	4.540	70.4602	48.0	2.9055	7.01	7.20	9.22	9.38
110.1000	1.5625	4.233	95.7674	64.0	2.7089	7.02	7.15	8.64	8.79
137.6250	1.5625	4.761	120.2386	80.0	3.0473	7.03	7.14		
165.1500	1.5625	4.965	145.0350	96.0	3.1777	7.04	7.13		
192.6750	1.5625	4.383	170.6170	112.0	2.8049	7.04	7.10	8.76	8.90
220.2000	1.5625	5.735	194.2649	128.0	3.6700	7.05	7.12		
1.0320	1.5625	0.769	0.1685	0.6	0.4923	8.40	10.04	9.36	9.36
1.3762	1.5625	0.971	0.2790	0.8	0.6215	8.42	9.94	9.38	9.38
1.7203	1.5625	1.193	0.3700	1.0	0.7634	8.41	9.90	9.46	9.46
3.4406	1.5625	1.957	1.1680	2.0	1.2525	8.37	9.58	9.47	9.47
6.8812	1.5625	2.573	3.6770	4.0	1.6465	8.41	9.27	9.38	9.38
13.7625	1.5625	3.000	9.5000	8.0	1.9201	8.27	8.86	9.14	9.14
27.5250	1.5625	3.737	21.2630	16.0	2.3918	8.42	8.82	9.44	9.44
82.5750	1.5625	4.015	70.9850	48.0	2.5695	8.29	8.43	9.24	9.24
110.1000	1.5625	3.840	96.1600	64.0	2.4578	8.39	8.47	9.15	9.15
137.6250	1.5625	4.571	120.4290	80.0	2.9251	8.42	8.49	10.11	10.11
165.1500	1.5625	4.789	145.2110	96.0	3.0650	8.34	8.40		
192.6750	1.5625	5.775	169.2250	112.0	3.6959	8.29	8.36		
								8.96[b]	9.39[b]
								CV (%) 216.22[c]	121.78[c]

[a] Units = M^{-n}. [b] Values are expressed as the log of the mean of the "K". [c] CV = coefficient of variation = the true standard deviation (not logarithmic) divided by the true mean multiplied by 100. Total zinc = protein-bound zinc + diffusible zinc Due to the equilibrium formulation, when $\bar{\nu}$ is greater than 3, a constant could not be calculated.

Scatchard analysis is used to determine the number of binding sites on a macromolecule, the "binding constant" is often calculated from the slope of the line. However, with the additional information we have gained for this protein, we are able to determine a stoichiometric constant.

In order to calculate a stoichiometric equilibrium constant for the protein–metal interaction, several parameters must be known: (1) the number of binding sites; (2) the nature of the binding sites (e.g., dependent, independent); (3) the amino acids involved in binding; and (4) the acid dissociation constants (pK's) of those amino acids involved. Our Scatchard analysis reported above offers no evidence for more than one type of binding site. Thus, the three binding sites appear to be equivalent and independent. The sequence of the N-ter-

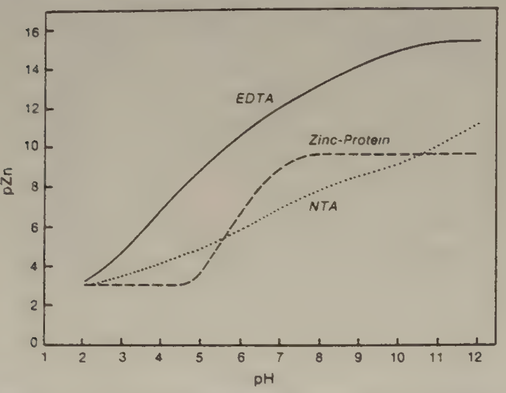

FIGURE 7: Free zinc ion concentration (expressed as $-\log [Zn^{2+}]$) computed as a function of pH in solutions of zinc and chelator (chelate:zinc ratio = 1.1:1). The zinc–ligand equilibria were solved for the following parameters: total zinc concentration, 1.0 mM; total ligand concentration (EDTA, NTA, or Zn protein), 1.1 mM; and association constant for the zinc–protein [$Zn(His)_3$ protein] complex, $10^{9.39}$ M^{-1}.

minal 30 amino acids of the protein shows a cluster of histidines and carboxylates, which we consider to be the most probable residues involved in binding. A full description of this work will be presented elsewhere. Two to four residues were used in our calculations, and every possible combination of the two types of amino acids at each pH was considered. Only two combinations listed in Table III (His_2 and His_3) yielded a reasonable fit with the experimental data. Only the inclusion of histidines affected the binding constant; the addition of carboxyl groups had an insignificant effect. Derivations of the apparent p*K*'s and equilibrium equations for calculating the stoichiometric binding constant have been calculated and are available upon request.

The mean of the computed stoichiometric equilibrium constants was $10^{8.96}$ for two histidines and $10^{9.39}$ for three histidines. The coefficient of variation of the data [(SD/mean) × 100] for three histidines involved in the binding was approximately half that for two histidines. The smaller relative coefficient of variation for the His_3 binding formulation indicates that this model gives a better fit with the data. Note that at pH 8.5 the log *K* values for two or three histidines are identical. At this pH, the histidines are fully deprotonated, and maximal binding is expected.

Strength of the Metal–Protein Chelate. The avidity of different chelators for a metal is best compared by displaying the concentration of uncomplexed (free) metal in the presence of excess chelator (Hegenauer et al., 1979). Because the association constant for the formation of a metal chelate is measured with respect to the fully dissociated ligand, uncomplexed metal will vary greatly depending upon pH. Therefore, it is inappropriate to judge the relative strength or affinity of metal binding solely by numerical comparison of association constants. However, we may display this competition between protons and metal by plotting free metal concentration as a function of pH. Figure 7 shows a comparison of pZn ($-\log [Zn^{2+}]$) computed at different pH values for zinc:chelator ratios of 1:1.1 for ethylenediaminetetraacetic acid (EDTA), NTA, and the albacore Zn protein. In this simulation, free zinc concentration in the presence of Zn protein reaches a minimum plateau beyond pH 8.0, where the histidines become fully dissociated. Between pH 5.7 and 10.5, the Zn protein is a better chelator than NTA and will accept zinc from the NTA chelate despite the fact that the numerical value of the association constant of NTA for zinc is approximately 30 times greater than the association constant of the protein for zinc.

DISCUSSION

The binding of zinc to macromolecules in the serum of mammals has been studied extensively (Giroux & Henkin, 1972; Prasad & Oberleas, 1970; Parisi & Vallee, 1970; Evans & Hahn, 1974). The two major serum proteins responsible for binding zinc are albumin and α_2-macroglobulin. Fletcher and Fletcher (1980) found an albumin-like Zn protein in the plasma of winter flounder which bound over 95% of the zinc in the plasma. We have identified and characterized a Zn protein in the plasma of albacore tuna which we believe to be similar to, if not identical with, that of the winter flounder. The albacore protein was the only protein in the plasma to show any significant zinc uptake. Our albacore protein is not albumin. It contains three times more histidine than human serum albumin (HSA) [16 residues for HSA (Henkin, 1974) and 48 for the albacore zinc protein (Table II)]. With a $\bar{\nu}$ of 3, the albacore protein binds 3 times more zinc than HSA (Giroux & Henkin, 1972). The affinity of the albacore Zn protein is 100 times greater than HSA [Giroux & Henkin (1972); HSA = 10^7; albacore zinc protein = 10^9; Table III]. We believe the albacore Zn protein can now be considered a new zinc transport protein.

This protein was also found in skipjack and yellowfin tuna plasma (unpublished experiments). Preliminary equilibrium dialysis experiments using strongly denaturing conditions (6 M urea) showed no loss of binding activity, indicating the binding site to be structural rather than conformational. Futher studies are under way to sequence the protein and elucidate the structure of the Zn site.

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OCEANOLOGICA ACTA, 1987, N° SP

Estimating ocean production from satellite-derived chlorophyll : insights from the Eastropac data set

Primary production
Satellite images of chlorophyll
Photoadaptation (of photosynthesis)
Mixing layer depth
Phytoplankton

Production primaire
Télédétection de la chlorophylle
Photo-adaptation
Couche de mélange
Phytoplancton

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ABSTRACT

The Eastropac expedition took place in 1967-1968 in the Eastern tropical Pacific Ocean. Primary production was related to near-surface chlorophyll in these data. Much of the variability in the relation was due to the light-history of the phytoplankton and its photoadaptive state. This was due to changes in the depth of mixing of the surface waters more than changes in insolation. Accurate estimates of production from satellite chlorophyll measurements may require knowledge of the temporal and spatial variation in mixing of this region.

Oceanol. Acta, **1987.** Proceedings International Symposium on Equatorial Vertical Motion, Paris, 6-10 May 1985, 109-113.

RÉSUMÉ

Estimation de la production océanique par télédetection de la chlorophylle : un aperçu des données « Eastropac »

Dans les données de la campagne Eastropac, qui s'est déroulée en 1967-1968 dans l'Est du Pacifique tropical, la production primaire est reliée aux concentrations superficielles en chlorophylle. Une grande partie de la variabilité de cette relation est le fait de l'exposition antérieure du phytoplancton à la lumière et de sa photo-adaptation, et ce conditionnement dépend davantage de la profondeur de la couche de mélange que des variations de l'insolation. L'estimation précise de la production primaire à partir de mesures satellitaires de la chlorophylle peut donc requérir, dans une telle région, la connaissance des variations spatio-temporelles de l'intensité du mélange vertical.

Oceanol. Acta, **1987.** Proceedings International Symposium on Equatorial Vertical Motion, Paris, 6-10 May 1985, 109-113.

INTRODUCTION

The coastal Zone Color Scanner (CZCS) aboard the Nimbus 7 satellite has for the first time provided large-scale views of near-surface chlorophyll-like pigments (Gordon *et al.*, 1983 : Hovis *et al.*, 1980), particularly of the coastal regions of North America. Within a few years satellite images of chlorophyll may be available for many regions of the ocean and hopefully for the global ocean (National Academy of Sciences, 1984). A second generation instrument to replace the CZCS is not yet funded as of this writing.

Characteristically these images have a large spatial scale. Potentially these images can also provide temporal coverage adequate to describe event scale and longer term phenomena. For example pigment changes near the Galapagos Islands were noted during the recent El Niño events (Feldman *et al.*, 1984). Satellite images were used also to study other interannual changes in pigments and primary production in the eastern equatorial Pacific (Feldman, 1986). Because of these prospects it is useful to ask whether primary productivity can be quantitatively reconstructed from the chlorophyll images in order to provide information relevant to biological resources of the ocean and to global biogeochemical cycles. Needed is a relationship of the form

$$\text{Production } (\text{mgC m}^{-2}\text{ d}^{-1}) = \\ = F \times \text{Pigment } (\text{mg m}^{-3}), \quad (1)$$

where Pigment is the near-surface, chlorophyll-like pigment and F is either a constant or a variable that can be constrained by environmental parameters.

Direct comparisons of ocean production with satellite-derived chlorophyll are few (Smith *et al.*, 1982). As an indirect approach to evaluating F we can compare primary production and chlorophyll in historical data from oceanographic cruises to examine the relations between primary production and near-surface chlorophyll and the temporal and spatial variations in such relationships. This report considers the Eastropac data collected in 1967-68 on chlorophyll and primary production in the eastern tropical Pacific, including the equatorial upwelling area (Owen, Zeitzschel, 1970 *a*).

Previous comparisons of primary production and near-surface chlorophyll have shown clear regional differences that may determine the choice among alternative strategies of estimating primary production from space. For example, in the central gyre of the North Pacific, near-surface chlorophyll is not correlated with primary production in the historical ship data (Hayward, Venrick, 1982). Production there varies by only a factor of two between stations, seasons and years, and a mean value, either of F or of primary production, might be adequate for most models of carbon flux. On the other hand, production is related to near-surface chlorophyll and to certain environmental variables in southern California coastal waters and the historical ship data suggest satellite chlorophyll data can be used effectively to estimate primary production (Eppley *et al.*, 1985), a conclusion reached also by comparing satellite chlorophyll with concurrent measures of chlorophyll and production (Smith *et al.*, 1982). Significant correlations have been found between primary production and surface chlorophyll in several studies (Lorenzen, 1970 ; Taniguchi, 1972 ; Smith, Baker, 1978 ; Eppley *et al.*, 1985) when data from disparate ocean regions were included in the correlations, but the predictive value of such coarse relations may not be great.

METHODS

The Eastropac expedition consisted of seven 2-month cruise periods from February, 1967 through April, 1968. The cruises covered an area between 20N and 20S and from the coast of America to 119W. We have limited our analysis to the offshore area bounded by 93W on the east, 119W on the west, and 300 km offshore on the north in order to emphasize the equatorial upwelling region (Fig. 1). The Eastropac data have been published in the form of atlases (Love, 1970-1977) which contain detailed cruise tracks and data in chart form. Primary production was measured with the ^{14}C method in noon to sunset, simulated *in situ* incubations (Owen, Zeitzschel, 1970 *b*). Samples from each of seven depths in the euphotic zone were incubated under neutral density screens at the temperature of surface seawater. The resulting rates were integrated over depth to express water column primary production mgC m^{-2} d^{-1}. This quantity is hereafter called Pi (Bannister, 1974). Chlorophyll and phaeopigments were measured using a fluorometer (Owen, Zeitzschel, 1970 *a*). Insolation was measured on the ships with pyrheliometers (Owen, unpublished). The stepwise linear regression program we used, number P2R, is from BMDP-83 (Dixon, 1983).

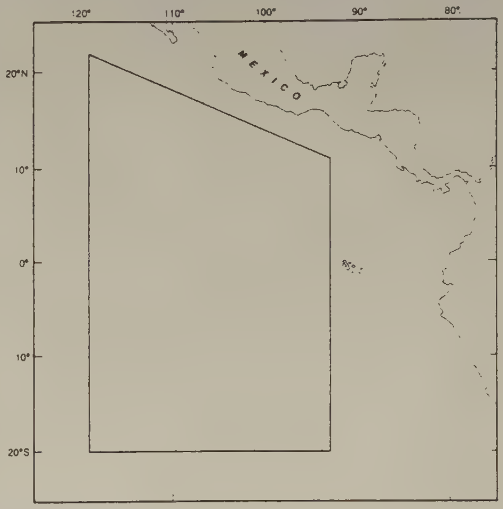

Figure 1

Map of the Eastern tropical Pacific. Stations used in this study were within the shaded area.

To estimate the chlorophyll-like pigments expected to be registered by the Coastal Zone Color Scanner and its successors, we calculated the average value of chlorophyll *a* plus phaeopigment for the upper two sampling depths, mg m^{-3}. This value is called Ck (Smith, Baker, 1978). We calculated the diffuse attenuation coefficient for light, Kt, by assuming the irradiance at the bottom of the euphotic zone equaled one percent of the surface value.

It is assumed that the 14C method of measuring primary production, as used in the Eastropac expeditions and elsewhere since 1952, provides an accurate measure of primary production during the incubation period. Thus the discrepancies between results with this method and those that integrate over larger space and time scales are due to an inadequate scale of sampling, a problem that may be overcome using satellite information.

RESULTS

Multiple regression model

Since present or future satellite data may include sea surface temperature, insolation, and winds from which the depth of mixing might be estimated, we used these variables (except winds) in stepwise multiple linear regression models of Pi. In the absence of wind data we used mixed layer depth, inferred from temperature profiles. The results were not impressive and at most only 34 % of the variability in Pi could be explained (Tab. 1). The second equation of Table 1 includes a parameter, Ic (a concept introduced by Myers and Graham, 1959), an estimate of the average irradiance experienced by a phytoplankter in the euphotic zone. Ic combines insolation, Kt and mixed layer depth in an analytical expression that has proved useful in studies of photosynthesis and growth of algal cultures (Tab. 1).

Table 1

Stepwise multiple linear regression equations for Pi (primary production, mg C $m^{-2}d^{-1}$), Ck (near-surface chlorophyll-like pigments, mg m^{-3}), Io (irradiance, watt m^{-2}), Kt (diffuse attenuation coefficient, m^{-1}), MLD (mixed layer depth, m), and Ic (mean irradiance experienced by the phytoplankton : $I_c = (I/Kt.MLD)\,(1-\exp{-Kt.MLD})$. Values in parenthesis represent the variance explained by the parameter.

$$\ln Pi = 6.90 + 0.722 \ln Ck\ (0.269) + 0.0010\ Io\ (0.033) - 8.50\ Kt\ (0.019) - 0.0043\ MLD\ (0.016) \qquad \text{Total } r^2 = 0.336$$

$$\ln Pi = 5.07 + 0.580 \ln Ck\ (0.269) + 0.245 \ln I_c\ (0.047) \qquad \text{Total } r^2 = 0.316$$

The Ck was the most important variable in these equations (Tab. 1). Ic explained about 5 % of the variability, only a bit more that insolation alone. Regression equations without the log transformation of variables explained less of the variability in Pi than those shown.

Analytical model

Bannister (1974) and Smith and Baker (1978) developed a simple model relating Pi and Ck to the photoadaptive state of nutrient-sufficient phytoplankton :

$$Pi = 2.3\ Pmax\ (Ck/Kt), \tag{2}$$

where Pmax is the highest rate of photosynthesis per weight of chlorophyll observed at some discrete depth in the water column. Figure 2 shows the result in the form of the identity Pi/Ck = F = 2.3 Pmax/Kt. The slope of the least squares regression line is 2.3, as predicted, and about 70 % of the variation in Pi is accounted for in the regression. We can draw two conclusions from Figure 2. First, variations in F are probably due to photoadaptation. The photoadaptive state of the plankton reflects its recent light history, that is whether the plankton grew in bright or dim light. Photoadaptation depends upon irradiance, daylength and the depth of mixing of the surface waters as those are the factors which determine the parameters of the photosynthesis-light curves of the plankton. They are expected to be correlated with F (Smith, Baker, 1978). Second, the fit implies that most of the light attenuation is due to plankton.

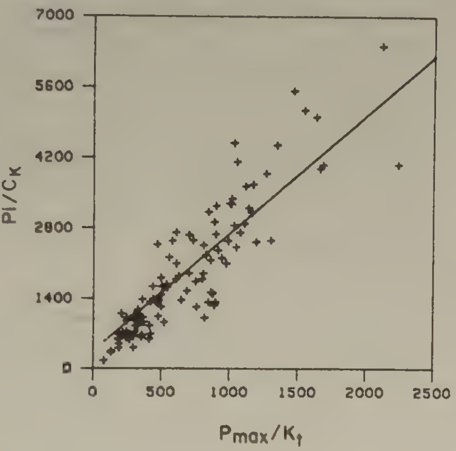

Figure 2

Variation in the ratio Pi/Ck (primary production/near surface chlorophyll-like pigments = F of equation 1) with the ratio Pmax/Kt (see text). Units of Pi are mgC $m^{-2}d^{-1}$, Ck mg m^{-3}, Pmax mgC (mg pigment)$^{-1}d^{-1}$, and Kt m^{-1}. Each point represents a station. The regression line slope was 2.3. The regression explained 71 % of the variation.

Variations between current systems

Blackburn *et al.* (1970) described the spatial and temporal variation in chlorophyll and Owen and Zeitzschel (1970 *a*) the corresponding variations in primary production before the stations could be assigned to discrete currents ; the geostrophic currents were described later (Tsuchiya, 1974). Table 2 shows the variation in F between the North Equatorial Current (NEC), North Equatorial Counter Current (NECC), and South Equatorial Current (SEC). The mean value of F was higher and the variability was greatest in the NECC and NEC. Both regions were outside the upwelling area as judged by the absence of nitrate at 10 m depth. Within the SEC, and at stations within about 1.5° latitude of the Equator, where no geostrophic flow could be assigned, F was about 1 200 (Tab. 2), nitrate was present at all these stations.

Table 2

Data from the Eastropac expedition, 1967-1968 : Pi (primary production mg C $m^{-2}d^{-1}$) ; Ck (near-surface chlorophyll-like pigments mg m^{-3}) and the ratio Pi/Ck ; mean (and standard deviation) for stations in discrete currents.

Current	No. stations	Pi	Ck	F = Pi/Ck
NEC	31	243 (136)	0.16 (.09)	1733 (1134)
NECC	21	194 (133)	0.16 (.07)	1450 (1254)
SEC	54	205 (105)	0.20 (.09)	1160 (638)
Equator	20	307 (159)	0.25 (.07)	1236 (636)

NEC = North Equatorial Current. NECC = North Equatorial Counter current
SEC = South Equatorial Current.

Equatorial stations with uniform chlorophyll over depth, and therefore with well mixed waters, showed the lowest values of F (about 600 ; the lower limit-value of F is about 100 ; Eppley *et al.*, 1985) while higher values, up to 2 400, were found in stratified waters with subsurface chlorophyll maxima. Stations in both the NEC and NECC showed a larger range in the variance of chlorophyll over depth, implying greater chlorophyll stratification, than in the SEC.

DISCUSSION

Highest values of F and greatest variability in Pi and Ck were found in the NEC and NECC where the waters were both oligotrophic, judged by the absence of nitrate at 10 m depth, and stratified. Conversely F was lowest in the nutrient-rich SEC. There, nutrients were in excess and were not likely to limit primary production. Rather, changes in primary production resulted from changes in stability and mixing ; production was reduced by a poverty of light rather than nutrients (Barber *et al.*, 1983 ; Menshutkin, Finenko, 1975 — cited in Vinogradov, 1981). The reduction in primary production during the 1982 El Niño event was due to a greatly increased mixing depth, rather than a lack of nutrients (Barber *et al.*, 1983).

The variability in the depth distribution of chlorophyll near the Equator and in the SEC generally suggests that even in the nutrient-rich equatorial waters of the eastern Pacific the intensity of vertical mixing must be patchy, as reported earlier from both biological (Vinogradov, 1981) and physical observations (Knox, Anderson, 1985 and references therein).

Improved models for estimating the intensity of mixing using satellite wind data may be possible. At present only about 34 % of the variability in Pi could be explained using our stepwise multiple linear regression model. Better estimates would require either *in situ* measurements of the intensity of mixing or of photosynthetic parameters such as Pmax. It is interesting that a goal of the TROPIC HEAT program is " ...to parameterize the turbulence in terms of larger scale quantities which are both easier to monitor and resolvable in model studies " (Eriksen, 1985). Attainment of this goal would also facilitate estimating primary production from satellite chlorophyll in the eastern tropical Pacific. Also, more extensive studies of primary production and chlorophyll variability in relation to hydrography have taken place in the tropical Atlantic. Variability has been examined on time scales from 24 hour (Le Bouteiller, Herbland, 1982), to several days (Herbland, Le Bouteiller, 1982) and seasons (Herbland *et al.*, 1983). Analysis of this data set is expected to increase significantly our understanding of the use of satellite data to estimate primary productivity in equatorial waters.

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Tuna aggregation and feeding near fronts observed in satellite imagery

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Abstract— Stomach contents of albacore (*Thunnus alalunga*) and skipjack (*Katsuwonus pelamis*) caught off California in August 1983 showed they were feeding on juvenile northern anchovy (*Engraulis mordax*), other fishes, and planktonic crustaceans. The distribution and diet of these predators were related to mesoscale frontal features visible in satellite sea surface temperature and phytoplankton pigment imagery. Albacore were caught in the vicinity of a filament of cold, pigment-rich surface water that varied with the intensity of coastal upwelling on time scales of several days. Stomachs of albacore caught closer to the filament contained relatively more juvenile anchovy and fewer pelagic red crabs (*Pleuroncodes planipes*). Skipjack were caught in warm water in the Southern California Bight, north of their normal range due to El Niño warming. They appeared to be feeding most successfully near the strong frontal boundary of a productive, cold water mass south of Pt. Conception, where dense patches of euphausiids were available. Both species were feeding near variable, mesoscale centers of high productivity where prey abundance may be enhanced.

INTRODUCTION

TUNAS are highly active foragers of fishes, squids, and large zooplankton. Their feeding behavior is a concern of fisheries scientists and managers because (1) predation is a major component of the natural mortality of their fish prey and may control recruitment in prey populations (ROTHSCHILD and FORNEY, 1979), and (2) migration and schooling behaviors involved in feeding affect the availability and catchability of tuna for important commercial and recreational fisheries.

LAURS *et al.* (1984) showed that albacore (*Thunnus alalunga*) aggregated along the coast near surface frontal boundaries associated with coastal upwelling. They speculated that the distribution of albacore in these waters was related to feeding activity. BERNARD *et al.* (1985) analysed stomach contents of albacore and skipjack (*Katsuwonus pelamis*) caught off central and southern California during August 1983. They found marked interspecific differences in feeding habits.

We re-examined the distribution of these tunas and variations in their feeding habits using the data set from the study of BERNARD *et al.* (1985), but on a smaller spatial scale at which satellite imagery reveals habitat variability. We hypothesized that active searching for aggregations of prey would result in differences in stomach contents associated with mesoscale environmental features that persist long enough to affect prey availability.

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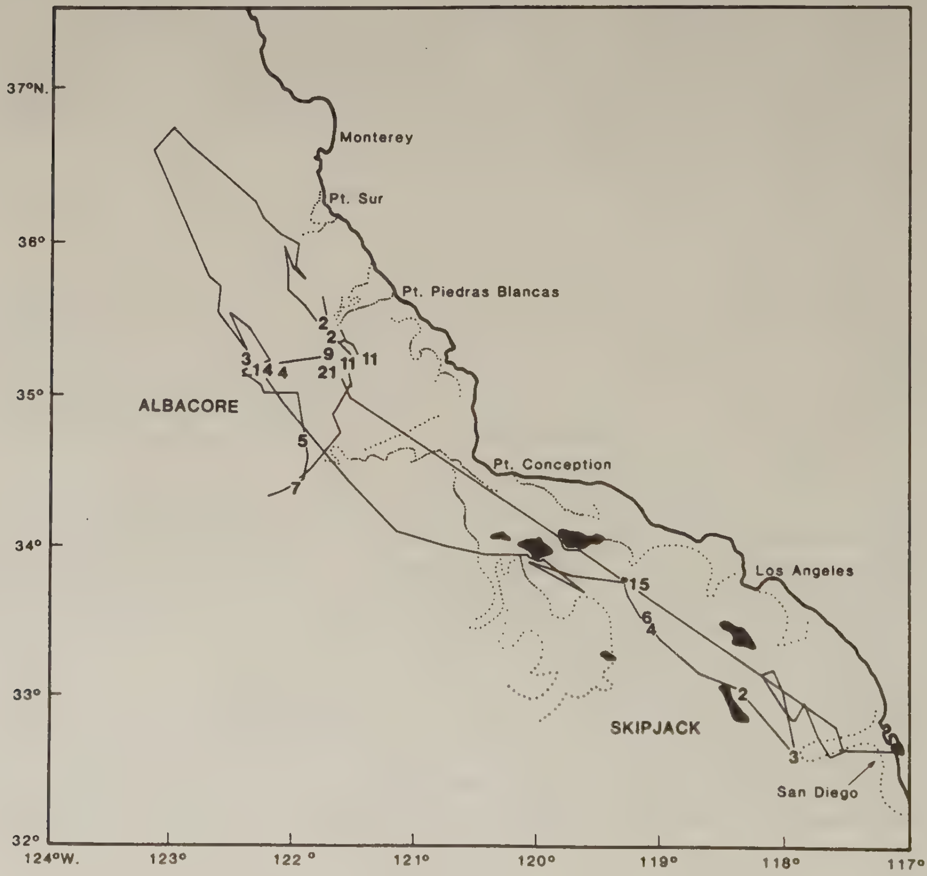
METHODS

Albacore and skipjack were sampled by nearly continuous daytime trolling during cruise 166 of NOAA ship *David Starr Jordan*, 15 August–1 September 1983 (Fig. 1). Analysis of stomach contents is described in Bernard *et al.* (1985). Stomachs were frozen aboard ship and returned to the lab where the contents were measured and rough-sorted. Northern anchovy were sorted from all other fish. These fish were not sorted further, although the presence of juvenile *Sebastes* spp. was noted.

Satellite data covering the California coast were received, archived, and processed at the Scripps Satellite Oceanography Facility (SSOF) of Scripps Institution of Oceanography in La Jolla, California. Daytime thermal infra-red data from channel 4 (11 µm) of the Advanced Very High Resolution Radiometer (AVHRR) on the NOAA-7 satellite were corrected for the effect of thin low clouds, using channel 2 (0.7–1.1 µm) near-infrared data (Gower, 1985). Visible radiance data from the Coastal Zone Color Scanner


37°N.
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119°
118°
117°
Monterey
Pt. Sur
Pt. Piedras Blancas
Pt. Conception
Los Angeles
San Diego
ALBACORE
SKIPJACK
2
2
9
11
11
21
3
14
4
5
7
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6
4
2
3
2

Fig. 1. Cruise track and catches of albacore (*Thunnus alalunga*) and skipjack (*Katsuwonus pelamis*) during cruise 166 of R.V. *David Starr Jordan*, 15 August–1 September 1983. Dotted line represents upwelling fronts visible in satellite imagery north of Pt. Conception on 25–26 August and south of Pt. Conception on 2 September.

(CZCS, on the Nimbus-7 satellite) were processed with an algorithm based on Gordon *et al.* (1983) to remove effects of Rayleigh and aerosol scattering and to derive pigment concentrations from corrected blue/green radiance ratios.

Spatial differences in predator and prey variables were tested by analysis of variance when possible. However, the highly skewed distributions of stomach content data required the use of the non-parametric Kruskal–Wallis test or, for variables with many zero values, chi-square contingency table analysis of differences between medians or frequencies of occurrence (Conover, 1971).

RESULTS

Albacore

Eighty-nine albacore were caught from 17 to 22 August in the vicinity of an upwelling filament at Pt. Piedras Blancas (Fig. 1). The series of AVHRR sea surface temperature images in Fig. 2 illustrates variability in the intensity of upwelling along the central California coast in response to changes in the strength of equatorward winds during August (Fig. 3).

On 4 August, coastal upwelling was well-developed following 15 days of strong upwelling-favorable winds (coastal upwelling index $>100\ m^3\ s^{-1}\ 100\ m^{-1}$). The coldest surface water is near Pt. Sur, but a long filament of cold water extended offshore from Pt. Piedras Blancas. On 8 August, upwelling-favorable winds were strengthening following a brief lull and coastal upwelling was still well-developed. August 15 was the last of 4 days of relatively weak winds (coastal upwelling index <50). Coastal upwelling appeared weak in this image, but the sea surface temperature pattern was partially obscured by dense atmospheric water vapor.

August 23 was the first day in 13 with strong upwelling-favorable winds. Cold, upwelled water was visible along the coast at Pt. Piedras Blancas and to the north. By 25–26 August, after a brief pulse of strong winds, upwelling filaments were developing both at Pt. Piedras Blancas and at Pt. Sur. An anticyclonic eddy south of Pt. Piedras Blancas was entraining warm water from the Southern California Bight south of Pt.

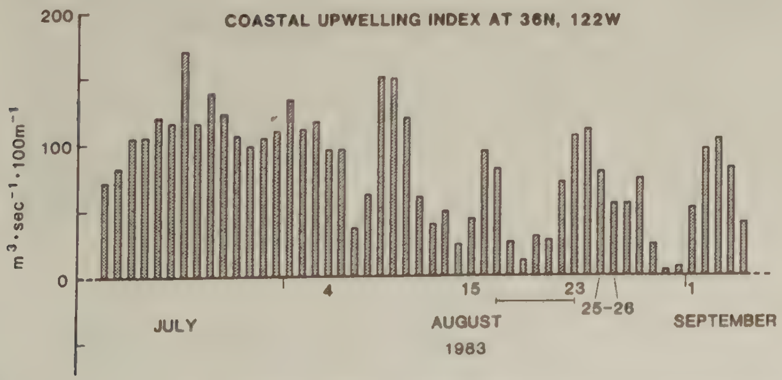

Fig. 3. Daily mean coastal upwelling indices, from alongshore winds in a 3° square centered at 36N, 122W (Pacific Fisheries Environmental Group, NOAA/NMFS/Southwest Fisheries Center, Monterey, California). Bar below abscissa indicates period of sampling north of Pt. Conception.

Conception. On 1 September, well-developed upwelling filaments were visible in spite of very weak winds over the previous 3 days.

During the period albacore were sampled, 15–22 August, equatorward winds and the surface pattern of cold, upwelled waters were not constant. Therefore, we grouped the sampled albacore by proximity to the upwelling filament at Pt. Piedras Blancas, based on the surface temperature where they were captured: near (16.5–17.0°C), intermediate (17.4–17.6°C), and far (18.1–18.3°C). Satellite-derived sea surface temperatures of the filament in Fig. 2 are 14–15.5°C.

Mean length and stomach volume of albacore increased with distance from the upwelling filament (Table 1). Eighty-two percent of the total number of prey items in albacore stomachs were fishes [35% juvenile anchovies of 22–47 mm SL and 47% other fish (Bernard *et al.*, 1985)]. Stomach fullness and prey composition varied greatly between individuals. For example, stomach fullness ranged between 4 and 73%. Stomachs with identifiable food sometimes contained only prey of a single type (e.g. anchovies, other fish, or pelagic red crabs), but more often contained two or more prey types.

Neither mean stomach fullness nor median total prey per albacore varied significantly with proximity to the filament. However, there were significant differences in prey composition: the numerical proportion of fish in the diet increased with proximity to the filament, anchovy were relatively more numerous in the stomachs of albacore caught near the filament, other fish were more numerous in albacore caught at intermediate distances and temperatures, and pelagic red crabs were more numerous in the diet far from the filament. No other prey category exhibited significant differences in relative numerical importance.

Table 1. Albacore (Thunnus alalunga) *size and diet differences with distance from upwelling filament*

	Near	Intermediate	Far	
Means				
Fork length (cm)	65.7 ± 2.0	72.8 ± 2.7	75.1 ± 3.7	$P < 0.01$
Stomach volume (ml)	90.0 ± 12.9	135.8 ± 20.0	141.9 ± 25.0	$P < 0.01$
Stomach fullness	0.35 ± 0.04	0.37 ± 0.07	0.32 ± 0.07	NS
Medians				
Total prey	27	25	19	NS
Fish/total	0.98	0.91	0.86	$P < 0.05$
Anchovies/total	0.55	0.00	0.11	$P < 0.01$
Other fish/total	0.30	0.67	0.06	$P < 0.10$
Crustaceans/total	0.014	0.000	0.059	NS
Frequencies of occurrence				
Pleuroncodes planipes	0.03	0.17	0.33	$P < 0.01$
Amphipods	0.26	0.14	0.27	NS
Euphausiids	0.21	0.22	0.07	NS
Other crustaceans	0.87	0.83	0.93	NS
Cephalopods	0.26	0.47	0.33	NS

Differences in mean length, stomach volume, and stomach fullness (±2 S.E.) were tested by one-way analysis of variance, median total prey by Kruskal–Wallis test, median relative numbers of prey categories by the median test, and frequencies of occurrence of other prey types by chi-square contingency table analysis. $n = 38$ near the filament, 36 at intermediate distances, and 15 far from the filament.

NS = Not significant.

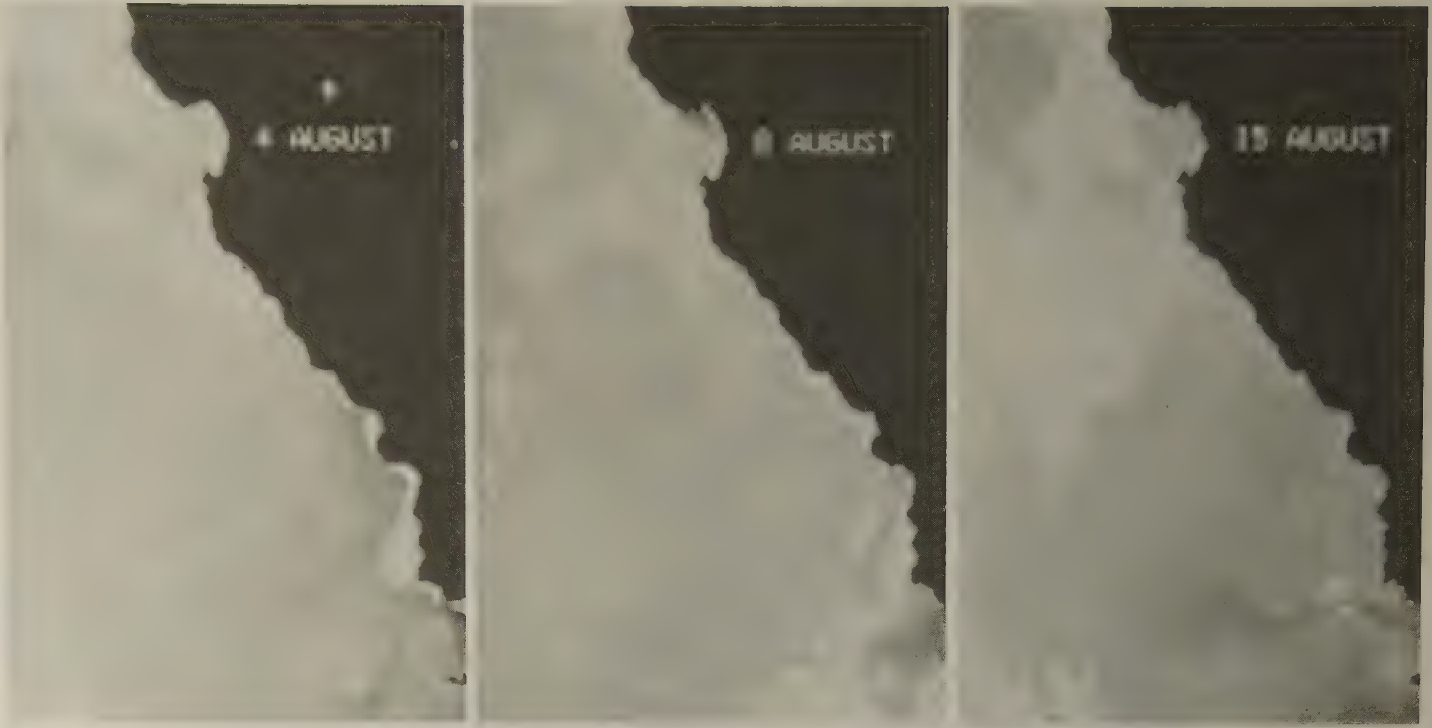

Fig. 2. Series of AVHRR sea surface temperature images of the central California coast during August 1983. In each image, Pt. Conception is at the lower right and Monterey Bay is near the top edge. Land is masked in black and clouds in white, with sea surface temperature increasing from light grey (~13°C) to dark grey (~18°C).

23 AUGUST

25/26 AUGUST

1 SEPTEMBER

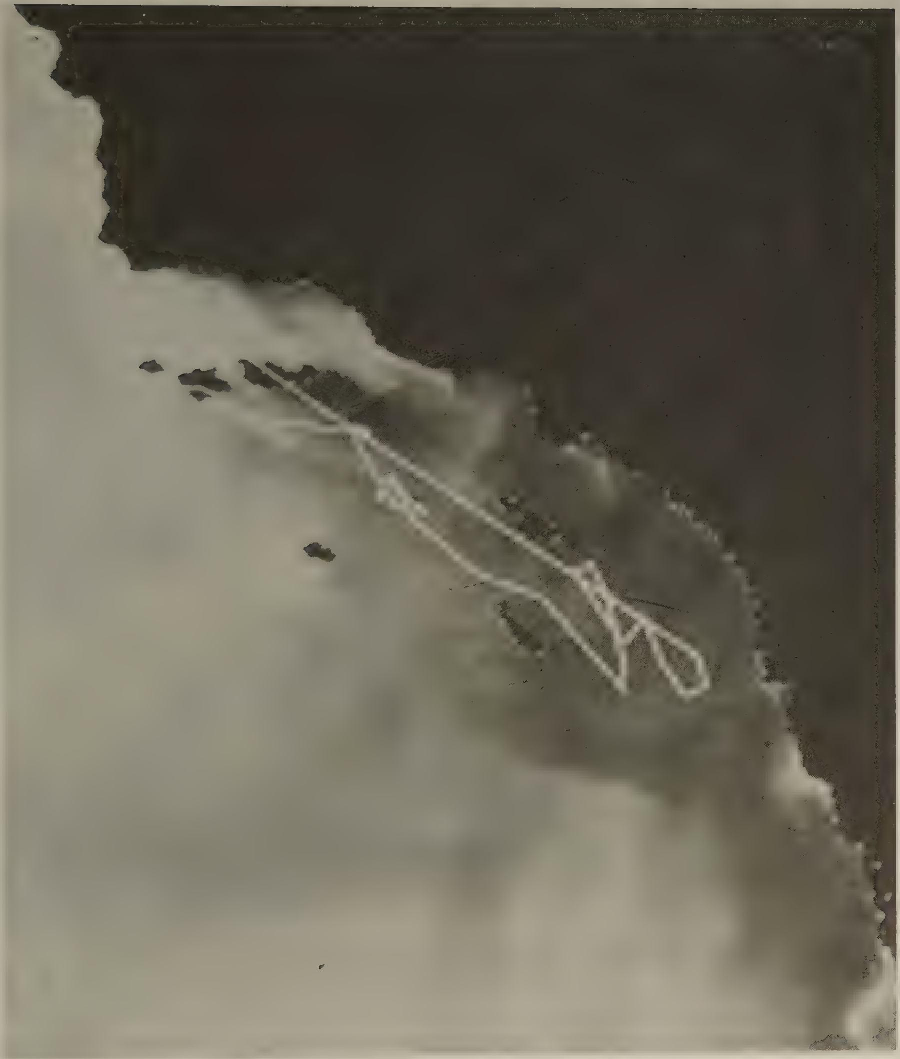

Fig. 4. AVHRR image of the Southern California Bight from 2 September 1983, masked as in Fig. 2. Sea surface temperature ranges from 13.5°C (light grey) to 22°C (dark grey).

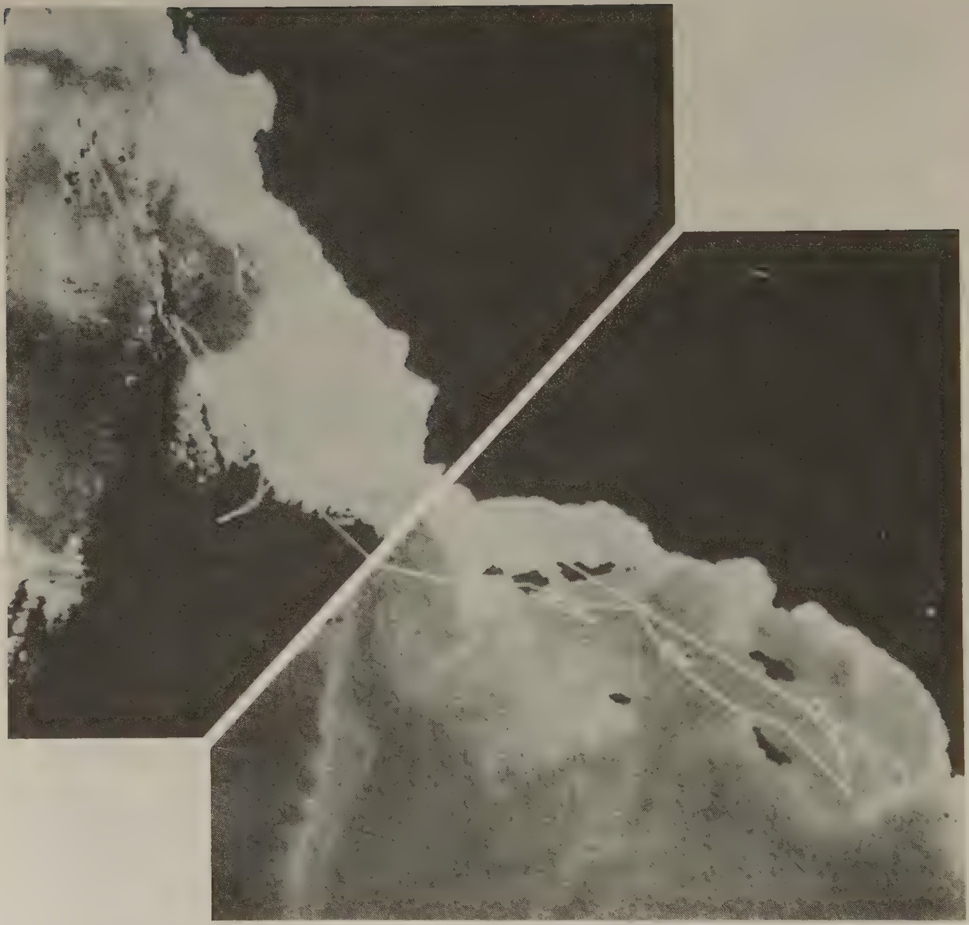

Fig. 5. CZCS images of central California (26 August 1983, top left) and Southern California Bight (2 September 1983, bottom right). Land and clouds are masked with black. Phytoplankton pigment concentrations range from 0.06 (dark grey) to 3.5 mg m $^{-3}$ (light grey).

Skipjack

In 1983, skipjack were caught in 20.9–22.4°C water in the Southern California Bight. Mean August surface temperatures in these waters are ≤18.5°C (Robinson, 1976). Skipjack were caught at two distinct sites (Fig. 1; temperature and pigment images in Figs 4 and 5). One group of 25 was captured near the edge of a consistently cool and productive water mass south of Pt. Conception. Another group of five was captured near a small upwelling squirt off San Diego (most obvious in the CZCS image, Fig. 5).

Eighty-six percent of the total number of prey items in skipjack stomachs were crustaceans, dominated by euphausiids (76%, primarily the coastal species *Nyctiphanes simplex*; Bernard *et al.*, 1985). The group of five caught near the weak upwelling squirt had a significantly greater proportion of empty stomachs (no identifiable prey items) than did the larger group (4 of 5 vs 6 of 25, $P < 0.25$, chi-square contingency table). We could not extend the comparison of food habits any further with one group containing only one stomach with identifiable prey.

DISCUSSION

Several aspects of the stomach content data examined by Bernard *et al.* (1985) may be interpreted as the result of "opportunistic" feeding. Exotic prey species, notably pelagic red crabs and the euphausiid *Nyctiphanes simplex*, were exploited as they became available off California during the anomalously warm summer of 1983. In that study and other studies of albacore feeding in the eastern North Pacific, diet composition varies both geographically and from year to year. Finally, the extreme non-randomness of counts of individual prey species in stomachs suggests exploitation of dense patches of prey.

The CZCS images in Fig. 5 illustrate that the cold, upwelled waters along the central California coast in Fig. 2 and to the south of Pt. Conception in Fig. 4 are rich in phytoplankton. The temperature fronts near which tunas were captured are also color fronts, or strong gradients in phytoplankton pigment concentration. This correspondence of temperature and color fronts is generally true of California coastal waters during the summer upwelling season. The productivity of the coastal water mass presumably supports an enhanced production at higher trophic levels, including prey populations exploited by tunas.

The diet of albacore caught nearest the upwelling filament at Pt. Piedras Blancas may reflect high availability of juvenile anchovy at that site. Juveniles are generally found close to shore in water <100 m (Messersmith *et al.*, 1969). This is inshore of the center of distribution of anchovy larvae (Hewitt, 1980). Albacore may have been sampling the cohort spawned in February–April as it moved onshore in late August. It is conceivable that offshore flow in the surface layer (upwelling) caused an accumulation of shoreward-moving anchovies. The pelagic red crabs consumed by albacore in warmer water far from the upwelling filament are rarely found this far north. The albacore were able to exploit this prey resource that had become available by a range extension during El Niño.

Skipjack are tropical tunas not normally found off California. During El Niño, their range expanded into the anomalously warm surface waters of the Southern California Bight. Blackburn (1969) found that skipjack off southern Baja California aggregated in waters warmer than 20°C where suitable food was abundant. During active upwelling, they aggregated at the edges of cool, high-chlorophyll areas where their principal prey, pelagic red crabs, were most abundant. The diet of the skipjack we sampled was also dominated by crustaceans, but by the euphausiid *Nyctiphanes simplex* rather than pelagic red crabs.

If the skipjack we sampled were aggregating to feed, their differential feeding success suggests that more of them had aggregated at the most favorable feeding site. Presumably, more prey were available near the consistently productive water mass off Pt. Conception than near the small upwelling squirt to the south.

Nyctiphanes simplex is a warm-water, coastal euphausiid. Point Conception is normally the northern limit of its range, with greatest abundances off southern Baja California (BRINTON, 1981). The range of *Nyctiphanes* had extended north at least to Monterey during zooplankton sampling along the coast of California on California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises in December 1983 and early 1984 (E. BRINTON, personal communication). In fact, *Nyctiphanes* was the most common euphausiid prey of juvenile coho salmon (*Oncorhynchus kisutch*) off Washington and Oregon during summer 1983 (PEARCY *et al.*, 1985), indicating a range extension of more than 1500 km. In the December 1983 CalCOFI samples, greatest abundances were observed along sampling lines in the vicinity of the Channel Islands, south of Pt. Conception in the Southern California Bight, where *Nyctiphanes* had been found in skipjack stomachs in late August.

Off Baja California, large numbers of *N. simplex* are often found in 13–14°C upwelled water near the coast (E. BRINTON, personal communication). This was the temperature of upwelled water in the Southern California Bight during El Niño. Large surface swarms have been observed during daylight off Baja California; this species exhibits little or no diurnal vertical migration. Therefore, it is likely that the skipjack found near the cold, productive waters in the vicinity of the Channel Islands were feeding on dense swarms of *Nyctiphanes*.

CONCLUSION

By using satellite imagery to reveal mesoscale habitat variability, we have documented two examples of feeding aggregations associated with oceanic fronts. Albacore aggregated to feed near a variable upwelling center of high productivity. Their diet was influenced by changes in prey availability with distance from this filament. Skipjack aggregated and fed most successfully near cool, productive waters where prey availability was high.

Both of these species had migrated to California coastal waters in the summer of 1983. Albacore migrate seasonally across the Pacific and exploit dense prey populations in the California Current during summer upwelling; skipjack had migrated to the Southern California Bight in response to anomalously warm surface temperatures during El Niño. Our observations demonstrate that aggregation at mesoscale coastal features of high productivity and prey availability is part of the feeding strategy of albacore and skipjack. The use of satellite temperature and color imagery to locate fishable aggregations of tunas is based on this feeding behavior.

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A POWER ANALYSIS FOR DETECTING TRENDS[1]

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Abstract. A power analysis allows estimation of the probability of detecting upward or downward trends in abundance using linear regression, given number of samples and estimates of sample variability and rate of change. Alternatively, the minimum number or precision of samples required to detect trends with a given degree of confidence can be computed. The results are applicable to an experimental situation in which samples are taken at regular intervals in time or space. The effects of linear and exponential change and of having sample variability be a function of abundance are investigated. Results are summarized graphically and, as an example, applied to the monitoring of the California sea otter population with aerial surveys.

Key words: *experimental design; linear regression; power analysis; trends.*

INTRODUCTION

A common proximate goal in ecological research is to determine whether the magnitude of some quantity is tending to increase or decrease. The quantity of interest might be population size, productivity, diversity, or mortality rate, for example. A linear regression of estimated abundance of the quantity against time or distance is commonly used to evaluate such a trend. When designing a program to detect trends, several related questions often arise. What is a sufficient number of samples? How precise must the samples be? What is the probability of detecting a trend if it is present?

This paper provides answers to these questions in terms which, it is hoped, are applicable to a wide range of ecological studies. The effects of several different factors are investigated, including the precision of the estimates of abundance, the dependence of precision on changes in abundance, the nature and magnitude of the actual rate of change in abundance, the asymmetry between upward and downward trends, and the levels of Type 1 and Type 2 statistical errors. Results are presented in both numerical and graphical form.

The ability of a statistical procedure to distinguish a situation different from the null hypothesis is called the power of that procedure. The estimation of statistical power is important for several reasons. Epistemologically, power analysis is important for the interpretation of results when the null hypothesis is not rejected (Toft and Shea 1983). Operationally, power analysis is important during the planning of experiments to avoid wasted time and effort on a program that is unlikely to yield useful information. Peterman and Routledge (1983), for example, showed that a proposed 48 million smolt/yr release would be insufficient to gain new information about the smolt–adult salmon relationship, while an alternative 88 million smolt experiment had a good chance of succeeding. Holt et al. (1987) used a power analysis to optimize the design of a large-scale program to detect changes in dolphin stocks over vast areas of the eastern tropical Pacific Ocean.

METHODS

By definition, a trend is detected when the regression has a slope significantly different from zero. The conclusion that a trend in abundance is occurring, when in fact it is not, is termed a Type 1 error, while the conclusion that no trend is occurring, when in fact it is, is a Type 2 error. The probabilities of making Type 1 and 2 errors are labelled α and β, respectively. Power is defined as $1 - \beta$.

I consider two simple models of change, linear and exponential. Let A_i represent abundance as a function of i, an index of time or distance. The linear model is

$$A_i = A_1[1 + r(i - 1)]. \qquad (1)$$

For each increment in i, abundance increases by a constant absolute amount rA_1. The parameter r thus expresses this constant increment of change as a fraction of the initial abundance A_1. The exponential model is

$$A_i = A_1(1 + r)^{i-1}, \qquad (2)$$

where r is the finite fractional rate of change per time or distance unit. A plot of A_i against i is an exponentially increasing (or decreasing) set of points; a plot of $\ln A_i$ against i is a straight line with slope $\ln (1 + r)$, the instantaneous rate of change.

Each abundance A_i is estimated by the sample abundance estimate $\hat{A}_i$. For the linear model (Eq. 1),

$$\hat{A}_i = A_i + \epsilon_i,$$

while for the exponential model (Eq. 2),

$$\ln \hat{A}_i = \ln A_i + \epsilon_i,$$

where the ϵ_i are normal, independent random variables

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TABLE 1. Theoretical dependence of the precision of an abundance estimate, as measured by the coefficient of variation (CV), on abundance (A), for some common methods of estimating abundance.

Method	Assumptions	Dependence	Reference
Quadrats/strip transects	random	CV $\propto 1/\sqrt{A}$	Seber (1982:22)
	clumped	CV $\propto 1/\sqrt{A}$	Seber (1982:25)
Line transects	random or clumped	CV $\propto 1/\sqrt{A}$	Burnham et al. (1980)
Distance sampling	random	CV constant*	Moore (1954)
	clumped	CV constant	Eberhardt (1967)
Catch per unit effort (CPUE)	random	CV $\propto 1/\sqrt{A}$	de la Mare (1984)
Single mark–recapture	Petersen method assumptions	CV $\propto \sqrt{A}$	Seber (1982:60)

* "CV constant" means the coefficient of variation does not depend on abundance, although it does depend on other parameters.

with mean zero. For the exponential model, note that this implies that the $\hat{A}_i$ are lognormally distributed. I consider three different assumptions about how the variance of the abundance estimate could be related to abundance: $\mathrm{Var}(\hat{A}_i)$ is proportional to A_i, to A_i^2, or to A_i^3. These relations can also be expressed in terms of the coefficient of variation, the ratio of the standard deviation to the mean: $\mathrm{CV}(\hat{A}_i)$ is proportional to $1/\sqrt{A_i}$, is constant with respect to A_i, or is proportional to $\sqrt{A_i}$, respectively. The nature of the dependence of $\mathrm{CV}(\hat{A}_i)$ on A_i will depend on the species, on the quantity whose abundance is of interest, and on the method used to estimate that quantity. The three assumptions made above span a range of functional relationships, and correspond to the theoretical dependences of $\mathrm{CV}(\hat{A}_i)$ on A_i for common methods of estimating abundance (Table 1).

Let n be the number of points used in the regression (the number of samples or estimates of abundance). In the case of linear change, the regression line is fitted to the points $\{y_i\} = \{\hat{A}_1, \hat{A}_2, \ldots, \hat{A}_n\}$, whereas for exponential change it is fitted to the points $\{y_i\} = \{\ln \hat{A}_1, \ln \hat{A}_2, \ldots, \ln \hat{A}_n\}$. Let

$$\hat{b} = \frac{\sum_{i=1}^{n} (x_i - \bar{x})(y_i - \bar{y})}{\sum_{i=1}^{n} (x_i - \bar{x})^2}$$

be the usual estimator of the slope of the regression line. Then $\hat{b}$ is normally distributed with mean $\mu_{\hat{b}} = b$ and variance $\sigma^2_{\hat{b}} = \sigma^2_{\mathrm{res}}/n\sigma^2_x$, where b is the true slope of the regression, σ^2_{res} is the variance of the residuals and σ^2_x is the variance in the independent variable x (Freund 1962:316). To reduce statistical errors to the specified levels α and β, we must have

$$|\mu_{\hat{b}}| - z_\beta \sigma_{\hat{b}} \geq z_{\alpha/2} \sigma_{\hat{b}}$$

or

$$b^2 n \sigma^2_x \geq (z_{\alpha/2} + z_\beta)^2 \sigma^2_{\mathrm{res}}, \tag{3}$$

where z_a is the value of a standardized random normal variable such that the area under one tail of the probability density function beyond z_a is a. If the null hypothesis is one-tailed, inequality 3 is modified to

$$b^2 n \sigma^2_x \geq (z_\alpha + z_\beta)^2 \sigma^2_{\mathrm{res}}. \tag{4}$$

To relate these equations to the problem of detecting trends, we need to express b, σ^2_x, and σ^2_{res} in terms of r, CV, and n.

For the linear model (Eq. 1), the slope of the regression line is

$$b = \frac{dA_i}{di} = rA_1. \tag{5}$$

If the estimates of abundance are taken at regular intervals in time or space, the independent variable x can, without loss of generality, be renumbered 1, 2, 3, ..., n. Then

$$\sigma^2_x = \frac{(n+1)(n-1)}{12}. \tag{6}$$

The variance of the residuals about the regression line depends on how $\mathrm{CV}(\hat{A}_i)$ changes with A_i. Let CV_1 be the coefficient of variation at the initial abundance A_1. If $\mathrm{CV}(\hat{A}_i)$ is proportional to $1/\sqrt{A_i}$, an estimate of the residual variance is

$$\begin{aligned}\hat{\sigma}^2_{\mathrm{res}} &= \frac{1}{n} \sum^{n} \mathrm{Var}(\hat{A}_i) \\ &= \frac{1}{n} \sum^{n} \mathrm{CV}_1^2 A_1 A_i \\ &= \frac{\mathrm{CV}_1^2 A_1^2}{n} \sum^{n} [1 + r(i-1)] \\ &= (\mathrm{CV}_1 A_1)^2 \left[1 + \frac{r}{2}(n-1)\right].\end{aligned} \tag{7}$$

Substituting Eqs. 5, 6, and 7 into Eq. 3,

$$r^2 n(n-1)(n+1) \geq 12 \mathrm{CV}_1^2 (z_{\alpha/2} + z_\beta)^2 \cdot \left[1 + \frac{r}{2}(n-1)\right]. \tag{8}$$

If $\mathrm{CV}(\hat{A}_i)$ is constant over the sampled range of A_i, write CV without the subscript. Then

$$\begin{aligned}\hat{\sigma}^2_{\mathrm{res}} &= \frac{1}{n}\sum^{n} \mathrm{Var}(\hat{A}_i)\\ &= \frac{1}{n}\sum^{n} \mathrm{cv}^2 A_i^2\\ &= \frac{\mathrm{cv}^2 A_1^2}{n}\sum^{n}[1 + r(i-1)]^2\\ &= (\mathrm{cv}A_1)^2\biggl\{1 + r(n-1)\\ &\qquad\cdot\left[1 + \frac{r}{6}(2n-1)\right]\biggr\}. \end{aligned} \tag{9}$$

Substituting Eqs. 5, 6, and 9 into Eq. 3,

$$\begin{aligned} r^2 n(n-1)(n+1) &\geq 12\mathrm{cv}^2(z_{\alpha/2} + z_\beta)^2\\ &\cdot\left\{1 + r(n-1)\left[1 + \frac{r}{6}(2n-1)\right]\right\}. \end{aligned} \tag{10}$$

If $\mathrm{cv}(\hat{A}_i)$ is proportional to $\sqrt{A_i}$,

$$\begin{aligned}\hat{\sigma}^2_{\mathrm{res}} &= \frac{1}{n}\sum^{n} \mathrm{Var}(\hat{A}_i)\\ &= \frac{1}{n}\sum^{n} \frac{\mathrm{cv}_1^2}{A_1} A_i^3\\ &= \frac{\mathrm{cv}_1^2 A_1^2}{n}\sum^{n}[1 + r(i-1)]^3\\ &= (\mathrm{cv}_1 A_1)^2\biggl\{1 + \frac{3r}{2}(n-1)\\ &\qquad\cdot\left[1 + \frac{r}{3}(2n-1) + \frac{r^2}{6}n(n-1)\right]\biggr\}. \end{aligned} \tag{11}$$

Substituting Eqs. 5, 6, and 11 into Eq. 3,

$$\begin{aligned} r^2 n(n-1)(n+1) &\geq 12\mathrm{cv}_1^2(z_{\alpha/2} + z_\beta)^2\\ &\cdot\biggl\{1 + \frac{3r}{2}(n-1)\biggl[1 + \frac{r}{3}(2n-1)\\ &\qquad + \frac{r^2}{6}n(n-1)\biggr]\biggr\}. \end{aligned} \tag{12}$$

Next consider the exponential model (Eq. 2). The slope of the regression line is

$$b = \frac{d \ln A_i}{di} = \ln(1 + r), \tag{13}$$

while the variance of x remains as before. Since the abundance estimates are log-transformed, we make use of the identity

$$\mathrm{Var}(\ln y) = \ln\left[\frac{\mathrm{Var}(y)}{[\mathrm{E}(y)]^2} + 1\right],$$

where y is lognormally distributed, which identity can be derived from the moment generating function of the normal distribution. If $\mathrm{cv}(\hat{A}_i)$ is proportional to $1/\sqrt{A_i}$,

$$\begin{aligned}\hat{\sigma}^2_{\mathrm{res}} &= \frac{1}{n}\sum^{n} \mathrm{Var}(\ln \hat{A}_i)\\ &= \frac{1}{n}\sum^{n} \ln\left\{\frac{\mathrm{Var}(\hat{A}_i)}{[E(\hat{A}_i)]^2} + 1\right\}\\ &= \frac{1}{n}\sum^{n} \ln\left[\frac{\mathrm{cv}_1{}^2}{(1 + r)^{i-1}} + 1\right]. \end{aligned} \tag{14}$$

Substituting Eqs. 6, 13, and 14 into inequality 3 gives

$$\begin{aligned} &[\ln(1 + r)]^2 n(n-1)(n+1)\\ &\quad \geq 12(z_{\alpha/2} + z_\beta)^2\left\{\frac{1}{n}\sum^{n}\ln\left[\frac{\mathrm{cv}_1^2}{(1 + r)^{i-1}} + 1\right]\right\}. \end{aligned} \tag{15}$$

If $\mathrm{cv}(\hat{A}_i)$ is constant with respect to A_i, we write cv without the subscript as before, and

$$\begin{aligned}\hat{\sigma}^2_{\mathrm{res}} &= \frac{1}{n}\sum^{n} \mathrm{Var}(\ln \hat{A}_i)\\ &= \ln(\mathrm{cv}^2 + 1) \end{aligned} \tag{16}$$

Note that this is the only case in which abundance estimates are truly homoscedastic. Substituting Eqs. 6, 13, and 16 into inequality 3,

$$\begin{aligned} &[\ln(1 + r)]^2 n(n-1)(n+1)\\ &\quad \geq 12(z_{\alpha/2} + z_\beta)^2[\ln(\mathrm{cv}^2 + 1)]. \end{aligned} \tag{17}$$

Finally, if $\mathrm{cv}(\hat{A}_i)$ is proportional to $\sqrt{A_i}$,

$$\begin{aligned}\hat{\sigma}^2_{\mathrm{res}} &= \frac{1}{n}\sum^{n} \mathrm{Var}(\ln \hat{A}_i)\\ &= \frac{1}{n}\sum^{n} \ln[\mathrm{cv}_1^2(1 + r)^{i-1} + 1]. \end{aligned} \tag{18}$$

Substituting Eqs. 6, 13, and 18 into inequality 3 gives

$$\begin{aligned} &[\ln(1 + r)]^2 n(n-1)(n+1)\\ &\quad \geq 12(z_{\alpha/2} + z_\beta)^2\\ &\qquad\cdot\left\{\frac{1}{n}\sum^{n}\ln[\mathrm{cv}_1^2(1 + r)^{i-1} + 1]\right\}. \end{aligned} \tag{19}$$

RESULTS

In this analysis, the detection of a trend has five parameters: n, the number of samples; r, the rate of change of the quantity being measured; cv, the coefficient of variation, a measure of precision; and α and β, the probabilities of Type 1 and 2 errors. Eqs. 8, 10, 12, 15, 17, and 19 relate these five parameters under different assumed models of change (linear or exponential) and different models of dependence of sample precision on abundance (cv constant, proportional to $\sqrt{A_i}$ or proportional to $1/\sqrt{A_i}$). Given any four of the parameters, the fifth can be found. If we are interested

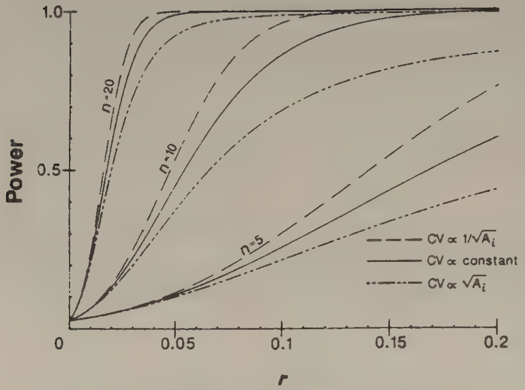

FIG. 1. Power of linear regression as a function of r, n, and the dependence of $\text{cv}(\hat{A}_i)$ on A_i. Curves shown use the linear model with $\text{cv}_1 = 0.2$ and $\alpha = 0.05$.

in the power of a certain procedure, for example, we solve for z_β, find β, and then compute power as $1 - \beta$.

In most cases, explicit solutions for r, n, or cv are not possible; iterative solutions on a computer are required. However, approximate solutions can be carried out on a hand calculator. For example, using the approximations

$$n(n - 1)(n + 1) \approx n^3$$

for moderately large integer n, and

$$\ln(1 + a) \approx a$$

for small a, Eq. 17 becomes

$$r^2n^3 \geq 12\text{cv}^2(z_{\alpha/2} + z_\beta)^2, \tag{20}$$

which can easily be explicitly solved for any of the five parameters. In fact, for small to moderate values of r, n, and cv, Eq. 20 serves as a useful approximation for any of the equations. For the common case where $\alpha = \beta = .05$, $(z_{\alpha/2} + z_\beta)^2 = (1.960 + 1.645)^2 = 13.0$, and an even simpler form useful for quickly relating r, n, and cv is

$$r^2n^3 \geq 156\text{cv}^2.$$

Figs. 1–3 present some of the detailed results graphically. In general, the figures show that power increases as r increases in absolute value (a stronger trend), as n increases (more samples), and as cv decreases (greater precision).

Fig. 1 shows how power is affected by the dependence of estimate precision on abundance. There are three sets of curves, for $n = 5$, 10, and 20. Power increases as n, the number of points used in the regression, increases. Within each set are three curves corresponding to the three assumptions of dependence of variability on abundance. There can be substantial differences in power among the different models, and these differences increase with cv (here set at 0.2). Within each set, power is highest—a trend is easiest to detect—when $\text{cv}(\hat{A}_i)$ is proportional to $1/\sqrt{A_i}$, but this order is reversed when $r < 0$, that is, when detecting a declining trend. Fig. 1 suggests that, at least for some combinations of parameters, it is important to know how precision will change as a function of abundance if power is to be correctly calculated. The three models explored here certainly do not exhaust possible functions, but they do span a range of possibilities. The choice of the most appropriate model of dependence may be made on theoretical (e.g., Table 1) or on empirical (e.g., Holt et al. 1987) grounds.

Fig. 2 contrasts linear and exponential models of change and the asymmetry between detecting increasing and decreasing trends. As in Fig. 1, there are three sets of curves corresponding to $n = 5$, 10, and 20. Within each set are four curves representing linear and exponential models, for increasing and decreasing trends. The power curves for exponential trends lie between the power curves for linear trends. In other words, between two trends that begin with the same amount of change, it is easier to detect an increasing trend in a quantity changing by constant proportional amounts than in one changing by constant absolute amounts, but the opposite holds for decreasing trends. Regardless of whether change is linear or exponential, decreasing trends are easier to detect than increasing ones, and the difference is particularly marked for linear change. For a linear decrease, note that abundance A_i becomes 0 for $i \geq 1 + 1/(-r)$. A trend will not necessarily be detected before A_i becomes 0 if the coefficient of variation is high.

Fig. 3 shows the effects of estimate precision on power, and contrasts one- and two-tailed tests of significance. The five pairs of curves, one for each value of cv, show that power decreases rapidly as the coefficient

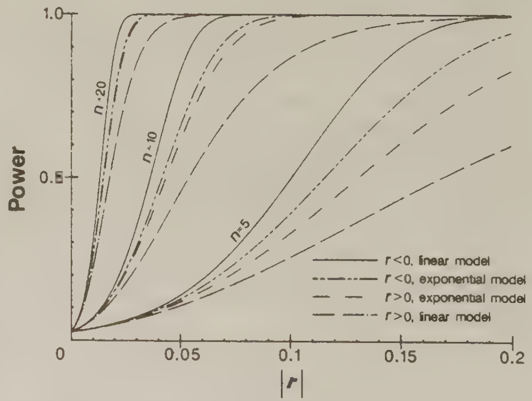

FIG. 2. Power of linear regression as a function of n, r (either >0 or <0), and linear vs. exponential models of change. Curves shown use the cv constant model with cv = 0.2 and $\alpha = .05$.

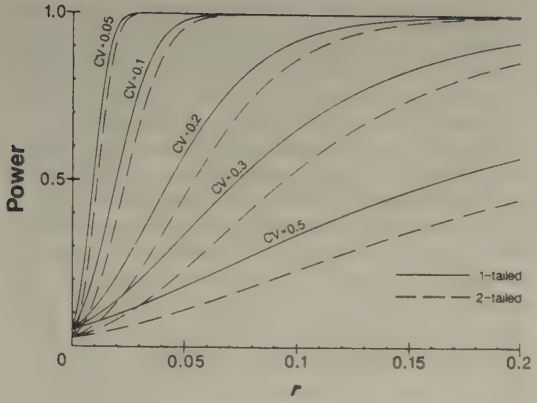

FIG. 3. Power of linear regression as a function of r, CV, and 1- vs. 2-tailed tests. Curves shown use the linear model with CV constant, $n = 10$, and $\alpha = .05$.

of variation increases; thus, the ability to detect a trend depends greatly on how precisely the quantity of interest can be measured. The solid lines show the increase in power if the null hypothesis is one-sided—in this case, that the trend is not increasing. Of course, this calculation of power applies only to trends that do in fact differ in the direction of the one-sided alternative hypothesis. A one-tailed test has no power to detect differences in the opposite direction. More concretely, if the one-sided null hypothesis H_0: "the trend is not increasing" is tested against the alternative H_1: "the trend is increasing," it is not possible to conclude that the trend is decreasing.

With minor reparameterization the results can be applied to some related problems of detecting trends. For example, the trend may be stated as an overall change in abundance of a given magnitude rather than as a rate of change per interval. That is, our question may be something like "What are the chances of detecting a trend if there is an 80% change in abundance between the first and last samples?" The results of this paper can be used if the 80% change is occurring uniformly between the first and last samples. Let R be the overall fractional change in abundance, and n the number of samples, as before. Then calculate r as

$$r = \frac{R}{n - 1} \tag{21}$$

for linear change, and as

$$r = (R + 1)^{1/(n-1)} - 1 \tag{22}$$

for exponential change. This is the rate of change r, per unit time or distance, that will lead to the specified overall change. Another related problem is a null hypothesis that the rate of change is some nonzero r^*. The equations and figures above still apply if r is replaced by $(r - r^*)$. The $100(1 - \alpha)$ percent confidence limits for an observed trend may be calculated as $r \pm z_{\alpha/2}\,\mathrm{SE}_r$, where the standard error is estimated by

$$\mathrm{SE}_r = \sqrt{\frac{12\hat{\sigma}^2_{\mathrm{res}}}{n(n + 1)(n - 1)}},$$

and $\hat{\sigma}^2_{\mathrm{res}}$ is calculated from Eq. 7, 9, 11, 14, 16, or 18, depending on choice of model.

If there is more than one sample taken per time or distance interval, the variance of the mean will be reduced. The coefficient of variation of the mean of m independent replicate estimates is $\mathrm{CV}/\sqrt{m}$, where CV is, as above, the coefficient of variation of a single estimate. If estimates are taken close together in time or space, however, they may not be independent, and $\mathrm{CV}/\sqrt{m}$ may be an underestimate. Correction for autocorrelation can in many cases be made by assuming the first-order autoregressive model

$$\epsilon_i = \rho\epsilon_{i-1} + \delta_i,$$

where $|\rho| < 1$ and the δ_i are independent random normal variables with mean zero and constant variance σ^2. Under this model, the observed variance of the error terms is

$$\sigma^2(\epsilon_i) = \frac{\sigma^2}{1 - \rho^2},$$

and estimation of CV may require a corresponding adjustment. Analysis of autocorrelated data requires modified regression techniques not discussed in this paper (see, for example, Neter et al. 1983).

NUMERICAL EXAMPLE

After being reduced to near extinction at the beginning of this century, the sea otter (*Enhydra lutris*) population in central California has gradually recovered. As the otter population has grown, so has pressure to manage the species. Otters strongly influence the composition of the nearshore community (Estes et al. 1978, VanBlaricom and Estes 1987) and, more particularly, greatly reduce the abundance of species highly valued by humans (lobster, crab, and abalone). There is considerable controversy about how to manage these marine mammals, but an important factor to consider in any management scheme is whether the population is currently increasing, decreasing, or remaining stable.

In order to judge the feasibility of monitoring sea otter population trends using aircraft, the United States Fish and Wildlife Service conducted a series of seven replicated strip transects during the winter of 1981–1982 to determine the precision of aerial counts. On the basis of these replicates, the coefficient of variation of a single count is estimated to be 0.13 (J. A. Estes, *personal communication*). The coefficient of variation of strip transects is proportional to the inverse of the square root of abundance (Table 1), and population growth is likely to be exponential. For these reasons, Eq. 15 is selected as the most appropriate equation to analyze the power of detecting future changes in population size. It is assumed that the data will be analyzed at the $\alpha = .05$ significance level (two-tailed).

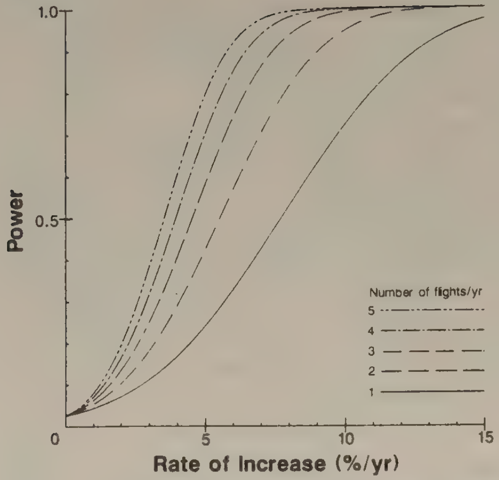

FIG. 4. Power curves for detecting various rates of annual increase in population size of sea otters in central California using five annual aerial surveys. More flights per year permit more precise estimates of population size, hence greater power to detect a given rate of increase.

Suppose a 5-yr monitoring program is contemplated. Fig. 4 shows power curves for detecting various rates of annual increase with different numbers of flights per year, under the assumption that the variance of the mean count is reduced in proportion to the number of flights. If a single flight is made each year, for example, the probability of detecting a 10%/yr increase in population size is 0.72. With 2 flights/yr, the coefficient of variation of the mean count is $0.13/\sqrt{2} = 0.092$, and the power increases to 0.95. Suppose we wish to know the probability of detecting a 30% increase in population size at the end of 5 yr. From Eq. 22, with $R = 0.3$ and $n = 5$, we calculate $r = 0.068$. With 1 flight/yr, the probability is only 0.4 of detecting the 30% increase, assuming the increase occurred smoothly over 5 yr. The probability of detecting a decrease of the same size is only slightly higher (cf. Fig. 2).

Let us ask how precise our samples must be to detect this 6.8%/yr increase in population size. To reduce Type 2 error to 0.05 or less (that is, to detect the trend in abundance with 95% confidence if it is occurring), we calculate that CV must be 0.061 or less. To achieve this precision by replication alone would require $(0.13/0.061)^2 = 4.5$, or 5 flights/yr. Precision might also be increased in other ways, such as careful training of observers, flying only under optimal sighting conditions, etc.

Next suppose that the time period is not fixed, but that we wish to know how many years will be required to detect a trend. Fig. 5 summarizes the situation if we again assume that Type 2 error must be reduced to 0.05 or less. For example, with 1 flight/yr and an annual rate of increase of 6.8%, the graph shows that $n = 7.9$. Thus, eight annual surveys (over a period of 7 yr) are required to detect the trend under the conditions given. Note that, because the number of annual surveys can only be a whole number, the ordinate in Fig. 5 should be read as the next largest integer. The number of annual surveys required to detect a trend rises sharply as the annual rate of change becomes small. Annual rates of increase in the otter population of <2%/yr would be very difficult to detect using aerial surveys.

We might also consider whether annual estimates are the optimal frequency of sampling. If population size is changing slowly, it might be better to conduct surveys only every 2nd or 3rd yr. As the interval between surveys increases, the effective rate of change per interval increases, and the number of surveys therefore decreases. Table 2 shows the number of surveys required for different intervals between surveys, assuming a 5%/yr increase in population size and 2 flights/yr. The number of surveys required, and therefore the number and cost of flights, could be reduced to half by conducting surveys once every 3 yr instead of annually in this example. But Table 2 also shows that the number of years which will have elapsed by the time the trend is detected increases from 7 to 9 years if surveys are conducted only once every 3 yr. Moreover, the total increase in population size which will have occurred by the time the trend is detected changes from 41% to 55%. How these less tangible costs, including the cost of ignorance of population size two years out of three, are weighed against the savings in actual flight costs depends on the research goals. For example, Allen (1980) pointed out that, when dealing with possible declines in populations of species which are already rare or endangered, the total percentage change which

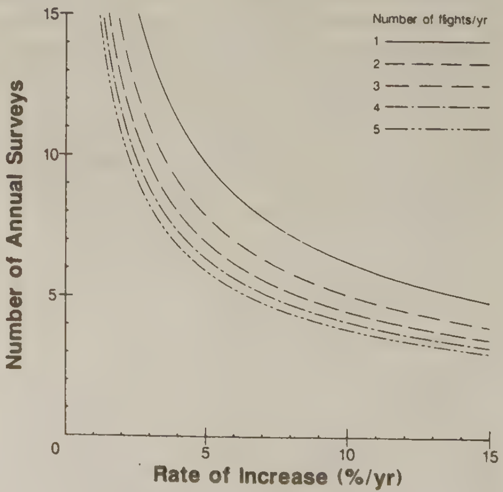

FIG. 5. Minimum number of annual surveys required to detect various rates of annual increase in population size of California sea otters. More flights permit more precise estimates of population size during each survey, hence fewer annual surveys required.

TABLE 2. Effects of different survey intervals on number of surveys required to detect a 5%/yr increase in sea otter population size. Also shown are several other quantities relevant to deciding on an optimal frequency of sampling this population.

No. yr between surveys (t)	No. surveys required* (n)	Effective % change/ interval ($1.05^t - 1$)	No. yr to detection† [$t(n - 1)$]	Total % change‡ [$1.05^{t(n-1)} - 1$]
1	8	5.0	7	41
2	5	10.3	8	48
3	4	15.8	9	55
4	4	21.6	12	80
5	3	27.6	10	63

* The required number of surveys is calculated from Eq. 15, assuming 2 flights/yr.

† The number of years that will have elapsed by the time the trend is detected.

‡ The total percentage change that will have occurred by the time the trend is detected.

will have occurred by the time a significant trend is detected may be the most critical factor to consider.

DISCUSSION

Statistical power is the probability that an analysis will reject a null hypothesis which is, indeed, false. Thus power is calculated as $1 - \beta$, where β is the probability of Type 2 error. In general, for any statistical test, power is a function of sample size (n), the probability of Type 1 error (α), and the magnitude of the difference between the null hypothesis and reality (the "effect size," Cohen 1977). Here effect size is quantified by the rate of change parameter r. In addition, we must consider that, in many ecological applications, measurement error is not trivial. This means that a practical power analysis must consider the uncertainty or variability associated with each estimate of abundance. That variability is parameterized by CV, the coefficient of variation of the estimate of abundance. These five parameters (CV, n, r, α, and β) are related by the equations derived in the Methods section. Which of the five parameters is of primary interest depends on the application.

There are two general situations in which a power analysis is useful: in experimental design, and in interpretation of results. When an experiment or sampling program is being designed, the questions most likely to be asked are: How many samples will be needed? How precise must the samples be? What is the probability of detecting a trend? These questions are answered by solving for n, CV, and β, respectively. Allen and Kirkwood (1976) analyzed the feasibility of detecting the results of experimental manipulations of whale stocks; they derive an equation similar to Eq. 17 and conclude that such a program is not practicable. When power analysis is used to aid in the interpretation of results, particularly when the null hypothesis is not rejected, the questions most likely to be of interest are: How large a trend could have been detected? What was the probability of detecting it? In this case, we solve for r and β.

The relations among these five parameters depend on assumptions made about the ecological process producing the trend and the techniques used to detect it. Models investigated explicitly in this paper include the assumptions that changes in abundance take place in constant increments (the linear model) or at a constant rate (the exponential model), and that the coefficient of variation is either constant, proportional to the square root of abundance, or proportional to the inverse of the square root of abundance. To apply the results of this paper one must decide which model most closely describes the situation at hand.

In general, the results show that the detection of trends depends strongly on the number and precision of the samples. Given a reasonable number of samples (say 10–15), CV must be sufficiently low, or r must be sufficiently high, to detect trends with controlled Type 2 error. We cannot control r, except indirectly by sampling at greater intervals, but we can control CV, at least the portion of it due to measurement error. CV can be reduced by expending greater sampling effort—more traps or greater areal coverage, for example. It can also be reduced by taking replicate measurements, since the mean of several independent measurements will have a lower variance than the measurements themselves, as illustrated by the sea otter example. It is difficult to generalize about what to expect the coefficient of variation to be, because that depends on the particular species involved, on what the quantity of interest is, and on what technique is used to estimate its abundance. Eberhardt (1978) discusses variability in a variety of techniques used in population studies.

A more subtle issue concerns balancing Type 1 and Type 2 errors. Other things being equal, there is a tradeoff between the levels of these two kinds of error. What error levels are acceptable depends on the research goals (Rotenberry and Wiens 1985). It is common practice to adopt .05 as the largest significance (α) level at which the null hypothesis is rejected, but there is no such common practice with regard to β, which is, by analogy, the level at which the null hypothesis is accepted. All too often, the null hypothesis is implicitly accepted without any consideration of power. If one is attempting to decide between a null hypothesis and a definite alternative, symmetry would dictate that α and β should be equal. The problem is that β, and its complement, power, is often not easily estimated. This paper allows β to be estimated for one commonly used statistical procedure, linear regression.

Some assumptions of this analysis may limit application of the results. The most restrictive assumption is that points are equally spaced along the x axis. This means that samples are assumed to be taken at regular intervals of time (daily, monthly, annually) or distance (every metre, kilometre, etc.). The results are robust to mild violations of this assumption, but if samples are clustered near either end of the *x* axis, quite different calculations of power could result. It is also assumed that the estimates of abundance are taken similarly each time, so that a single coefficient of variation suffices to describe all samples, and that, as a corollary, all samples are given equal weights in the regression. In some applications weighted regressions will be more appropriate, or will give lower estimates of variance (de la Mare 1984).

Another important assumption is that estimates of abundance are independent. This is a particular concern for time series, where estimates temporally close to each other may tend to be more similar than estimates far apart in time. Such positive autocorrelation means that residual variance may be seriously underestimated. This has important consequences. If studies are designed based on an underestimated variance, the power of detecting a trend will be less than planned (inflated Type 2 error). And if data with positive autocorrelation are analyzed by ordinary least squares. a trend may appear to exist when in fact it does not (inflated Type 1 error). Harris (1986) reported simulations that violated the assumption of independence, as well as other assumptions of detecting trends. He emphasized that for data collected under typical field conditions, analytical calculations will tend to underestimate the standard error of the regression line. The prudent investigator, therefore, should consider that the equations of this paper give minimum estimates of the number of samples *n* required, minimum estimates of the magnitude of the trend *r* which could be detected, and maximum estimates of the coefficient of variation CV which would permit it to be detected.

The a priori specification of variability of the samples is one of the most difficult problems when power analysis is used in experimental design. There are two general sources of variability: measurement error, and real variation in the parameter. In an ecological context, real variation means that, even if we could measure without error, points would never lie precisely along a straight line, either because of natural environmental variability in time or space, or because the processes that produce the trend do not act in an exactly linear or exponential manner. Although these two sources of variability are distinct conceptually, they are often difficult to separate in practice. Fortunately, it is not necessary to separate them for this analysis; both types of variability can be combined in the parameter CV. The problem lies in specifying CV correctly to reflect both types. If replicate measurements are taken, the resulting variance is an estimate of measurement error, and is a minimum estimate of the variability to be expected about the regression line because it does not include real variation. If CV is estimated from residual variance about the regression line, this will include real variability as well as measurement error, but of course such information will be available only after data have been collected. This is important for interpreting results, but for planning purposes, we would like to have an estimate of expected precision before the sampling program is begun. To make planning more realistic, some additional variability due to the environment should be included. If separate estimates of variance due to measurement error and to real variation are available, they can be combined. Let CV_m be the coefficient of variation of measurement error and CV_r the coefficient of variation due to real variability in the rate of change parameter *r*. Then the combined CV that would be appropriate to use in the equations above is

$$\mathrm{CV} = \sqrt{\mathrm{CV}_m{}^2 + \mathrm{CV}_r{}^2 + \mathrm{CV}_m{}^2\mathrm{CV}_r{}^2}.$$

To make the discussion less abstract, consider the detection of a trend in population size over time. The population dynamics of many insects, birds, small mammals, and marine animals with pelagic larvae are very sensitive to environmental conditions. The recruitment or production of new individuals can fluctuate substantially from one year to the next, depending on how favorable the environment is; in other words, there is real variation in *r*. If we wish to use the power analysis of this paper to detect a mean trend in population size, it will be important that the estimate of CV include this real variation, which may well be more important than measurement error. If we are unable to estimate the real variation in *r*, application of the results will be limited for such species. On the other hand, the population dynamics of large-bodied mammals and birds. certain fish, and some other organisms are characterized by damped variation in the population growth rate because reproduction is spread over many age classes. Such species approximate more closely the assumption of a constant growth rate. CV will mainly reflect measurement error, and since measurement error will usually be easier to estimate than future environmental variability, the results of this paper will be more readily applied to such species.

The use of linear regression analysis to detect a trend assumes that the change in abundance is linear, or has been made linear by suitable transformation of the axes. Frequently, however, the processes underlying the trend are but dimly perceived. The two simple models of change considered here, linear and exponential, are two ways in which abundance of a quantity could change regularly over time and space. In the absence of more detailed information to the contrary, the linear model is usually assumed in practice. The exponential model is frequently used for growth or decay processes. If another model is known to be more appropriate for a particular situation, a power analysis similar to the one presented here could be carried out for such another model. The usual situation, however, is that little is known about how the quantity of interest is changing over time or space—indeed, this is the motivation of the sampling.

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Trophic relationships among tropical seabirds at the Hawaiian Islands

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Introduction

Seabird communities in tropical and subtropical waters are often composed of large numbers of species that have complex trophic relationships. For example, 17 species breed on Laysan Island, Hawaii (Ely & Clapp, 1973) and 18 species breed on Christmas Island (Pacific) (Schreiber & Ashmole, 1970); trophic relationships are probably more complex than those in cold-water communities because of the larger number of food species available.

An important characteristic of tropical and subtropical zones is a relative lack of seasonal change in surface waters. Ryther (1963) and Ashmole (1971) defined these zones to include all areas where sea surface temperatures remain above 23°C all year. More precise definitions are probably impossible. A permanent thermocline is usually present which limits vertical enrichment of the euphotic zone throughout the year. Nutrient depletion in tropical oceans results in low primary productivity. This phenomenon is more pronounced in oceanic areas than near continents because land-based nutrients in neritic zones can increase productivity (Raymont, 1966).

Seabirds have adapted to life in tropical waters in various ways. Whereas cold-water species of a genus frequently have multi-egg clutches, tropical species often lay a single egg, presumably because the relatively impoverished food supplies allow fewer young to be raised successfully (Lack, 1967). Cold-water species tend to breed at predictable times each year to maximize the advantages of a seasonal abundance of food and to minimize the effects of cold weather and storms on vulnerable young. In contrast, tropical species often have ill-defined breeding seasons because they do not face severe winter weather and have fewer predictable feeding opportunities. Non-seasonal breeding occurs with many tropical species and at various locations (Nelson, 1979). Tropical seabirds have adopted foraging strategies that minimize contact with predatory fish such as tunas, sharks, and billfish that eat birds. They plunge rather than dive (Ainley, 1977), which restricts feeding to surface waters, and prey largely on epipelagic fauna (Harrison & Hida, 1980). Tropical oceanic areas do not have seasonal abundances of food that would attract vast numbers of migratory birds. Most migrant seabird species avoid tropical and subtropical areas and fly through them quickly to spend their non-breeding period in polar or subpolar areas (Ainley & Boekelheide, 1984). For example, Sooty and Short-tailed Shearwaters *Puffinus griseus* and *P. tenuirostris*, from the southern hemisphere migrate to Alaska to forage during their non-breeding season (Harrison, 1982), but few stop to feed in the tropical Pacific (King, 1970). These shearwaters are important consumers on migration in the colder water systems of California (see Chapter 12) and Oregon (Wiens & Scott, 1975).

From 1977 to 1983 we studied the ecology of Hawaiian seabirds to discover how they might be influenced by the growing fishery. Research on the biology of important commercial fishes has also helped to clarify the role of Hawaiian seabirds in the marine ecosystem. In this chapter we review the trophic relationships among Hawaiian seabirds and compare these with other tropical and subtropical seabird communities, discuss fishery interactions, and suggest directions for future research.

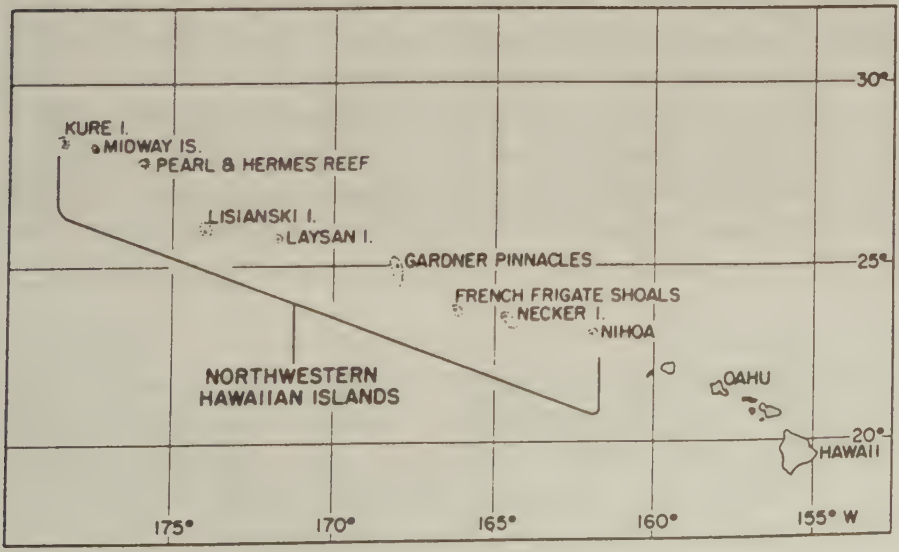
The Hawaiian Archipelago

We concentrated our work in the Northwestern Hawaiian Islands (NWHI) where 18 seabird species (two albatrosses, two shearwaters, one storm petrel, two petrels, three boobies, one frigatebird, one tropicbird, and six terns) breed. The NWHI are subtropical, extending from latitude 23° N to 28° N and longitude 162° W to 178° W in the North Pacific (Fig. 13.1). This location has several important influences on the seabird community. Many species are at or near the northern limit of their breeding range. The depth of the mixed layer is much shallower than in the main Hawaiian Islands (Hirota *et al.*, 1980), and the NWHI are often in the path of North Pacific winter storms. Apparently the food supply is seasonal. Fish larvae are much more abundant during summer than winter (Hirota *et al.*, 1980). Like the situation around Tahiti (Rougerie & Chabanne, 1983), the migratory tunas are much more abundant in Hawaii during summer (Waldron, 1964). These factors are presumably responsible for the tendency for seabirds to breed during summer, although albatrosses and petrels are important exceptions (Harrison, Hida & Seki, 1983).

Resource partitioning

The diets of Hawaiian seabirds are very complex. Representatives of 56 families, 86 genera, and 74 species of fish were found in the diets of the 18 species that breed in the NWHI (Harrison *et al.*, 1983). Numerous squid families and various groups of crustaceans were also represented in their diets. As previously, we group the seabirds of the NWHI into five guilds based on similarities in composition of diet, size of prey taken, and feeding strategies. These guilds are the albatrosses, pelecaniforms, terns and shearwaters that associate with predatory fishes, nocturnal petrels, and neuston-feeding terns. We acknowledge that tropical seabirds do not fit neatly into these categories and there are some difficulties with the characterization. For example, boobies and frigatebirds occasionally feed in association with tunas; however, they occur only with about 1% of the tuna schools sighted in Hawaiian waters (National Marine Fisheries Service (NMFS), unpublished data). Sooty Terns *Sterna fuscata* and Wedge-tailed Shearwaters *Puffinus pacificus* occasionally feed at night (Gould, 1967). Our information suggests that these feeding strategies do not

Fig. 13.1. The Hawaiian Archipelago.


30°
KURE I.
MIDWAY IS.
PEARL & HERMES REEF
LISIANSKI I.
LAYSAN I.
GARDNER PINNACLES
25°
FRENCH FRIGATE SHOALS
NECKER I.
NIHOA
NORTHWESTERN
HAWAIIAN ISLANDS
OAHU
20°
HAWAII
175°
170°
165°
160°
155° W

represent modal feeding behaviour in Hawaiian waters, and we have ignored such details in our analysis.

Albatrosses

Black-footed and Laysan Albatrosses *Diomedea nigripes* and *D. immutabilis*, eat primarily squid, flyingfish eggs, and deep-water crustaceans (Table 13.1). Many of the crustaceans and squid that were consumed possess photophores and may be bioluminescent at night. At least eight squid families were identified, but Ommastrephidae was the most common. When adequate keys are developed to identify squid beaks in Hawaii, it will be interesting to determine the differences and similarities between these birds with respect to squid predation. The proportions of prey consumed by each congener was very different. By volume, Laysan Albatrosses consumed twice as much squid, and Black-footed Albatrosses ate 11 times more flyingfish eggs. The differences in diets may result from the apparent tendencies of Laysan Albatrosses to feed at night and of Black-footed Albatrosses to feed during the day. Both species forage in the cool waters north of the NWHI, much farther from the islands than other seabirds in this community. Their feeding locations suggest a tenuous relationship with the tropical marine environment.

The albatross guild in Hawaii can be compared with the Waved Albatross *D. irrorata* in the Galapagos Islands, the only other tropical albatross. Like Hawaiian birds, Waved Albatrosses eat primarily squid, fish, and deep-water crustaceans (Harris, 1973). The squid families consumed in Hawaii, however, were different from those consumed in the Galapagos, where mostly representatives of Histioteuthidae and Octopoteuthidae are eaten. These squid families are rarely taken by Hawaiian birds, who feed predominantly on ommastrephid squid. The differences in the composition of squid in the diets may be attributed to the availability of the representative squid families to the birds at the different localities. Galapagos birds consume flyingfish and mackerel scad *Decapterus* spp., but no flyingfish eggs. The guild in Hawaii is therefore broadly similar to the only other tropical albatross, but there are some notable differences.

Pelecaniformes

The Red-footed Booby *Sula sula*, Brown Booby *S. leucogaster*, Masked Booby *S. dactylatra*, Great Frigatebird *Fregata minor*, and Red-tailed Tropicbird *Phaethon rubricauda*, comprise this guild. Adult flyingfish (especially *Exocoetus volitans* and *Cypselurus* spp.) were the most commonly taken prey, but adult mackerel scad and juvenile ommastrephid squid were also very important components of the diet (Table 13.1). Members of this guild have diets with different percentage compositions of major prey items and consume prey of different sizes. Masked Boobies took the largest prey; the mean prey length was almost twice that of the other species. Masked Boobies frequently took fish larger than 20 cm. The other birds consumed prey primarily in the 8–15 cm range, although Brown Boobies took many 5 cm juvenile goatfish (Mullidae). Red-footed Boobies, an offshore species, ate much more squid than Brown Boobies, an inshore species. Flyingfish were especially common (> 60% by volume) in the diet of Great Frigatebirds. Frigatebirds have a structural inability to take flight from the ocean's surface and therefore do not enter the water. Certain prey were taken exclusively by a single species at one location when presumably such prey was abundant. For example, virtually all Pacific Saury *Cololabis saira* were taken by Red-footed Boobies during the winter months at the northern end of the archipelago.

Table 13.1. *Average percent volumes for major prey (families or groups that constitute 2% or more of the volume of a guild) items of Northwestern Hawaiian Islands birds*

Prey	Albatrosses	Pelecaniforms	Terns and shearwaters associated with predatory fishes	Nocturnal petrels	Neuston-feeding terns
Carangidae	17.8	9.8	—	—	—
Clupeidae	—	—	2.2	—	2.7
Coryphaenidae	—	2.9	—	—	2.0
Exocoetidae	25.1	44.3	10.2	—	10.2
Hemiramphidae	—	4.2	—	—	—
Mullidae	—	3.6	20.8	—	8.9
Myctophidae	—	—	—	10.2	—
Ostraciontidae	—	—	—	—	21.1
Scombridae	—	2.5	—	—	—
Sternoptychidae	—	—	—	10.8	—
Synodontidae	—	—	4.9	—	7.4
Other fishes	4.2	8.8	19.1	24.4	24.1
Squid	48.2	13.2	30.2	23.5	2.7
Crustaceans	6.6	—	—	5.6	10.6
Marine insects	—	—	—	—	9.7
Unidentified remains	11.0	—	—	—	12.9

This guild may be compared with seabird communities at Ascension Island (Stonehouse, 1962; Dorward, 1963), Christmas Island (Ashmole & Ashmole, 1967; Schreiber & Hensley, 1976), the Seychelles Islands (Diamond, 1974, 1984), Rose Atoll (Harrison, Hida & Seki, 1984), and the Galapagos Islands (Harris, 1969). It consumes primarily flyingfish and ommastrephid squid throughout its range, but inshore feeding Brown Boobies have much greater diet diversity (Diamond, 1984). In Hawaii, this guild is distinguished by the prominence of juvenile goatfish and adult mackerel scad in the diet.

Terns and shearwaters associated with predatory fish

This guild includes many of the most common tropical seabirds: the Sooty Tern, Brown Noddy *Anous stolidus*, Black Noddy *A. tenuirostris*, White Tern *Gygis alba*, Wedge-tailed Shearwater, and Christmas Shearwater *Puffinus nativitatis*. These species feed largely in association with predatory fishes, especially tunas (Murphy & Ikehara, 1955; Waldron, 1964; Ashmole & Ashmole, 1967; Erdman, 1967). Recent observations in the eastern tropical Pacific indicate little feeding in the absence of fish schools (R.L. Pitman, personal communication).

Juvenile forms of goatfish, ommastrephid squid (especially *Symplectoteuthis* spp.), mackerel scad, and flyingfish were the main prey consumed by this guild (Table 13.1). Black Noddies and to a lesser extent White Terns feed inshore in association with the jacks *Caranx* spp. and nearshore tunas (e.g. *Euthynnus affinis*). Consequently, inshore-feeding terns eat more herrings Clupeidae and juvenile lizardfish Synodontidae and somewhat fewer mackerel scads and squid than the remaining birds in this guild. The offshore-feeding Sooty Terns, Brown Noddies, Wedge-tailed Shearwaters, and Christmas Shearwaters associate with Skipjack Tuna *Katsuwonus pelamis*, Yellowfin Tuna *Thunnus albacares*, and Dolphinfish *Coryphaena hippurus* (Table 13.4). Squid account for 30–50% of the dietary volumes of the offshore birds. The mean prey length of shearwaters, the heaviest species in this guild, is almost twice that of the lightest tern. For many of the common prey taxa, all species in the guild took similar size classes, usually 3–8 cm. This guild takes prey much smaller than that consumed by pelecaniforms. Feeding techniques account for some resource partitioning. Shearwaters can pursue prey underwater, whereas terns feed at the surface and rarely wet their feathers. Feeding locations may account for many of the differences among the diets of these species, but detailed information does not exist. Seasonal variation was apparent in the diet of each species in this guild.

The Hawaiian guild consumes higher proportions of fish than squid compared with guilds of Ascension Island, Christmas Island (Ashmole & Ashmole, 1967), and the Seychelles (Diamond, 1984). Hawaiian birds generally eat fewer flyingfish, substituting goatfish and mackerel scad. The Seychelles are the only other location where the latter two families are important components of the diet.

Nocturnal petrels

The Bonin Petrel *Pterodroma hypoleuca*, Bulwer's Petrel *Bulweria bulwerii*, and Sooty Storm Petrel *Oceanodroma tristrami*, apparently feed extensively at night. Each species feeds offshore in surface waters, usually alone but occasionally in association with other birds. This guild feeds primarily on squid, hatchetfish Sternoptychidae and lanternfish Myctophidae (Table 13.1). Most of their prey possess photophores and occur in surface waters only under reduced light conditions (Harrison *et al.*, 1983). Food samples from this guild are usually in very poor condition, making identification to genus or species difficult. Timing of breeding may be an important means to avoid competition for prey resources. Bulwer's Petrels breed during summer whereas Bonin Petrels and Sooty Storm Petrels breed during winter. Bulwer's and Bonin Petrels take larger prey than the storm petrels. They also consume more fish than squid, whereas the storm petrels take fish and squid in equal volumes. Improved identification technique for midwater fish may enable a better understanding of resource partitioning among the species in this guild.

Few comparisons with other tropical areas are possible because little work on these or similar species is published. Great-winged Petrel *Pterodroma macroptera* in New Zealand consumed similar midwater fish but different families of squid (Imber, 1973). Phoenix Petrels *P. alba* at Christmas Island ate 78% squid and 14% fish (Ashmole & Ashmole, 1967). Bonin Petrels are unusual among *Pterodroma* because they eat primarily fish rather than squid.

Neuston-feeding terns

The Gray-backed Tern *Sterna lunata* and Blue-gray Noddy *Procelsterna cerulea* have somewhat similar diets and, unlike other terns in Hawaii, rarely feed in association with predatory fishes. They feed inshore and take small prey during the breeding season. Their diets are remarkable because of the very small proportion of squid (Table 13.1). Their primary preys were marine insects (*Halobates sericeus*), crustaceans, and juvenile forms of Cowfish *Lactoria fornasini*, flyingfish, goatfish, and lizardfish. Their diets differed widely in the proportions of several taxa. Gray-backed Terns feed far more on Cowfish, whereas Blue-gray Noddies feed far more on marine insects (Cheng & Harrison, 1983) and lizardfish. Some competition is avoided because of slightly different breeding seasons: Blue-gray Noddies feed most of their young in March–May and Gray-backed Terns feed their young in May–July. In addition, Gray-backed Terns feed throughout the NWHI, but Blue-gray Noddies are restricted to the southern islands because of an absence of suitable breeding habitat elsewhere. Gray-backed Terns are larger birds and take somewhat larger prey than the noddies.

Neuston-feeding terns are little studied elsewhere. Blue-gray Noddies on Christmas Island have similar diets to Hawaiian birds in regard to the consumption of *Halobates* and minute crustaceans. However, Hawaiian birds ate goatfish and lizardfish and Christmas Island birds ate tunas, blennies, and snake mackerels (Ashmole & Ashmole, 1967).

Consumption of major prey items

It is very difficult to measure directly the amount of food that seabirds consume (Furness, 1982). Consequently, we have developed a model to estimate the energy and food requirements of the NWHI seabird community.

Table 13.2. *Recent population estimate of seabird breeding pairs in the Hawaiia*

	Main Hawaiian Islands	Kaula	Nihoa	Necker	French Frigate Shoals	Gardner Pinnacles
Diomedea nigripes	0	25–50	40–60	200–250	2000–2250	0
D. immutabilis	10	30–70	1–5	800–900	900–1000	10–15
Pterodroma phaeopygia	400–600	0	0	0	0	0
Pt. hypoleuca	0	0	0	0	30–50	0
Bulweria bulwerii	500–1000	20–50	75000–100000	250–500	200–500	10–15
Puffinus pacificus	40000–60000	1500–2500	30000–40000	1500–2500	1500–1750	50–100
P. nativitatis	40–60	75–125	200–250	0	15–20	0
P. puffinus newelli	4000–6000	0	0	0	0	0
Oceanodroma castro	+	0	0	0	0	0
O. tristami	0	0	2000–3000	+	+	0
Phaethon rubricauda	200–400	250–400	250–300	100–150	550–600	20–23
P. lepturus	500–3000	0	0	0	0	0
Sula dactylatra	3–4	200–400	250–300	250–300	500–600	125–150
S. leucogaster	75–100	300–500	150–200	20–25	40–60	5–10
S. sula	900–1200	250–350	1500–2000	650–750	550–600	0
Fregata minor	5–10	250–350	3500–4500	700–900	350–375	0
Sterna lunata	10	500–600	9000–12000	3500–4500	750–1000	1500–2500
S. fuscata	60000–90000	35000–50000	10000–25000	12500–25000	60000–78000	250–500
Procelsterna cerulea	0	?	2000–2500	1000–1500	+	+
Anous stolidus	15000–20000	15000–25000	25000–35000	10000–15000	5000–7500	1000–1500
A. tenuirostris	300–800	20–30	1000–5000	300–500	750–850	200–300
Gygis alba	50–100	30–40	1000–5000	100–300	500–750	150–250

The model was largely developed by Pettit, Whittow & Ellis (1984) and was expanded to encompass the entire NWHI seabird community. Estimates will be refined in the future as improved date become available.

Model methods and input

The model includes a component for adult maintenance energy. An estimate of the energy required for daily existence for each of the 18 species in the NWHI community was multiplied by the total number of days each year that each species is associated with the breeding islands. This amount was then multiplied by the total number of birds on each island. The estimate of daily existence energy includes the energy for foraging based upon gliding flight. It is particularly difficult to estimate the costs of foraging flight, yet we recognize it to be an extremely important component of the model (Furness, 1982). More than 5 million seabirds breed in Hawaii. The populations of each species and island are presented in Table 13.2. Non-breeding populations are included in this model and have been estimated as a percentage of the known breeding population, ranging from 31% to 70% (Fefer *et al.*, 1984). Tropical seabirds moult throughout the year, and this model assumed that daily existence energy requirements reflect the daily cost of moulting.

Archipelago (from Harrison et al., 1984, where full references are given)

Laysan	Lisianski	Pearl & Hermes Reef	Midway	Kure	
14000–21000	2800–3800	8000–11000	6500–7500	700–1300	*Diomedea nigripes*
105000–132000	23000–30000	9000–12000	150000–200000	3000–4000	*D. immutabilis*
0	0	0	0	0	*Pterodroma phaeophgia*
50000–75000	150000–250000	400–600	2500–5000	400–600	*Pt. hypoleuca*
1000–2000	50–100	< 10	0	0	*Bulweria bulwerii*
125000–175000	10000–30000	5000–10000	500–1000	900–1100	*Puffinus pacificus*
1500–2000	400–600	< 10	25–50	20–30	*P. nativitatis*
0	0	0	0	0	*P. puffinus newelli*
0	0	0	0	0	*Oceanodroma castro*
500–2500	?	300–500	0	?	*O. tristrami*
1500–2500	900–1300	10–60	4000–5000	1000–1300	*Phaethon rubricauda*
0	0	0	1	0	*P. lepturus*
400–425	300–350	140–160	5–10	65–75	*Sula dactylatra*
34	15–25	50–60	0	50–60	*S. leucogaster*
700–800	350–450	40–60	450–500	400–450	*S. sula*
2000–2500	750–850	300–400	60–75	200–250	*Fregata minor*
5000–10000	15000–20000	650–750	100–200	30–50	*Sterna lunata*
375000–500000	400000–600000	35000–45000	30000–45000	8000–12000	*S. fuscata*
0	0	0	0	0	*Procelsterna cerulea*
10000–15000	7500–15000	1700–2000	500–1000	700–800	*Anous stolidus*
1500–2500	500–1000	75–125	2000–6000	0	*A. tenuirostris*
1000–2000	50–100	10–20	5000–7500	5–10	*Gygis alba*

Added to the adult maintenance energy in the model is a component that estimates the costs of producing an egg. This was determined using bomb calorimetry and estimations of the efficiency of egg production. We assumed that birds laid a single egg and that each breeding pair produced one egg per year. The cost of producing an egg was then multiplied by an estimate of the number of eggs laid each year for each species. The amount of energy expended in raising a chick was estimated using growth equations and chick weight data. This amount was then multiplied by the number of chicks raised, using the highest observed reproductive success for that species in the NWHI (Pettit *et al.*, 1984).

The food requirement for each species was determined by use of volumetric estimates of the percentage of the diet for each prey species for each seabird (Harrison *et al.*, 1983). These estimates were converted into estimates of food consumption by using bomb calorimetric data for common prey items. The estimates of food consumed were calculated individually for each species and later pooled into feeding guilds.

Model results and discussion

Seabirds in the NWHI consume 410 000 tonnes of fish, squid, crustaceans, and other food sources each year (Table 13.3). Squid is the largest component, comprising over 54% of the total consumption. Fish accounts for 35% of the prey consumption of this community, the most important families being Exocoetidae (7%), Mullidae (5%), and Carangidae (primarily mackerel scad) (4%). Most of the squid were Ommastrephidae, especially *Symplectoteuthis oualaniensis*, but the large amount of unidentified squid in the albatross diets (Harrison *et al.*, 1983) makes this conclusion tentative.

Two feeding guilds account for almost all of the prey consumed. Albatrosses take 264 000 tonnes (64%) and birds that feed in association with predatory fishes consume 117 000 tonnes (29%). For individual species, Laysan Albatrosses account for 60% of the consumption. Laysan Albatrosses, Black-footed Albatrosses, Bonin Petrels, Wedge-tailed Shearwaters, and Sooty Terns together account for 94% of the prey consumed. Each of these birds consumes a large proportion of squid. The impact of neuston-feeding terns on the marine ecosystem is trivial, as biological intuition might suggest, but the minor role of pelecaniforms (2%) is unexpected.

It is interesting to compare the estimates of prey consumed by the NWHI seabird community with the present and projected fishery landings in the Hawaiian Archipelago. Although fish landings fluctuate each year and may be under-reported by as much as a factor of two. 6100 tonnes were reported as landed in 1978. The most optimistic estimates for increased fishery landings are 34 000–53 000 tonnes (Swerdloff, 1980). Hawaiian seabirds take 67 times the current reported landings of commercial fish in Hawaii, and more than seven times the highest projected fishery yields. Clearly seabirds are a very important component of the marine ecosystem in Hawaii, as they take more than a trivial quantity of the production of lower trophic levels. For example, an ecosystem model applied at French Frigate Shoals estimates that seabirds consume 42% of the annual production of small surface pelagic fishes and squid (Polovina, 1984). Several potential errors complicate this estimate of total food consumption. The largest is the population estimate of non-breeding seabirds. This population is very difficult to estimate accurately (Fefer *et al.*, 1984) and accounts for almost two-thirds of the consumption estimated by this model. In addition, there is considerable imprecision in the breeding

Table 13.3. *Annual consumption (thousand tonnes) of major prey (families or groups that constitute 2% or more of the volume of the diet of a guild)*

Prey	Albatrosses	Pelecaniforms	Terns and shearwaters associated with predatory fishes	Nocturnal petrels	Neuston feeding terns	Total
Carangidae	—	1.1	15.6	—	—	16.7
Clupeidae	—	—	0.2	—	0.1	0.3
Coryphaenidae	—	0.2	0.1	—	0.1	0.4
Exocoetidae	14.8	5.1	8.9	0.1	0.1	29.0
Hemiramphidae	—	0.4	0.1	—	—	0.5
Mullidae	—	0.1	20.2	0.6	0.1	21.0
Myctophidae	—	—	1.6	4.5	—	6.1
Ostraciontidae	—	—	—	—	0.5	0.5
Scombridae	—	0.2	—	—	—	0.2
Sternoptychidae	—	—	—	2.6	—	2.6
Synodontidae	—	—	0.8	0.3	—	1.1
Other fishes	6.8	0.8	16.0	0.9	0.2	24.7
Squid	167	1.3	51.4	3.4	0.1	223.2
Crustaceans	22.2	—	0.4	1.2	0.1	23.9
Unidentified remains	28.6	—	1.1	3.7	—	33.4
Other	25	0.1	1.0	0.3	—	26.4
Total	264.4	9.3	117.4	17.6	1.3	410.0

population estimates. Many species are very difficult to census. Nesting in the NWHI is often protracted over several months, and the colonies are remote and difficult to visit. We have inadequate knowledge of the budgets of adult foraging activites and do not know their feeding locations. Most estimates of feeding distances from colonies are speculation (Harrison & Stoneburner, 1981). It is important to learn the extent of foraging so that an area can be defined to estimate fish production.

These estimates of the amounts of food taken by seabirds are the first for a subtropical or tropical community. Seabirds play as important a role in tropical waters as they do in temperate areas. Wiens & Scott (1975) estimated that seabirds consume as much as 22% of the annual production of pelagic fish in Oregon. Schaefer (1970) estimated that seabirds in Peru consume 2.8 million tonnes of anchovies each year (one-third of the commercial catch) and account for 20% of the fish mortality (Furness & Cooper, 1982). Seabirds at one colony in Shetland, Scotland, consume about 29% of the fish production within a 45 km radius of the colony. Seabirds in the Benguela region take about 30% of the mean annual catch in the adjacent fishing grounds and about 17% of the annual fish production (Furness & Cooper, 1982). Primary productivity in Hawaii is about 36 g C m^{-2} (Hirota *et al.*, 1980), or 12–36% of the productivity of continental shelf or upwelling areas (Ryther, 1963). To the extent that fish production can be correlated with primary productivity, Hawaiian seabirds may consume a greater percentage than those in other areas.

Fishery interactions

Do seabirds in Hawaii compete with commercial fishermen? Because much of the NWHI remains unexploited, it is difficult to compare this community with areas that have established fisheries. Tropical ecosystems are complicated by the migratory nature of tuna stocks and other prey, including squid. It is difficult to define a discrete ecosystem, and annual fish production estimates could be misleading. The juvenile forms of fish and squid that comprise much of the food consumed by seabirds are below the trophic levels that would directly affect commercial fisheries. Prey of the seabirds may also be forage for commercial fish. Commercial fisheries for large species might result in increased forage for seabirds, as has occurred in the North Sea (Furness, 1982). Fishery–seabird competition is most severe when humans and birds compete for identical species in identical size classes (Idyll, 1973). The situation in tropical waters is greatly complicated by the dependency of many birds on tunas to drive their prey to the surface.

Bird flocks and predatory fish

The occurrence of terns and shearwaters in flocks provides invaluable assistance to tuna fishermen. Gould (1971) estimated that a trained observer could see and recognize a large feeding flock at a distance of at least 8 km and stated that some fishermen use the distinctive feeding patterns of birds as clues to determine the species of tuna feeding below the flock. If the flocking birds remain active low over the water, they are believed to be feeding over surface-feeding Skipjack Tuna. If the flock activity alternates between low and high altitudes, the fish beneath are presumed to be the deeper-foraging Yellowfin Tuna.

Between 1953 and 1969, the Southwest Fisheries Center Honolulu Laboratory, NMFS, NOAA (formally Pacific Oceanic Fishery Investigations (POFI) and the Bureau of Commercial Fisheries (BCF)) conducted tuna pole-and-line research cruises around the Hawaiian Islands aboard the research vessel *Charles H. Gilbert*. On these cruises, observations of bird flocks and fish schools were recorded using the scouting method (described and evaluated by Royce & Otsu (1955)) by which an experienced fisherman logs all observations of bird flock (as well as solitary individuals) and fish schools. During the *Gilbert* cruises (with at least 30 flock observations) 2138 bird flocks were investigated and 681 (32%) of the fish schools under these flocks were identified (Table 13.4). Tunas constituted 88% of the identified schools, and 86% of these tuna schools were composed of Skipjack Tuna. Because actual fishing verified the composition of schools, the high proportion of unidentified schools (68%) is not unusual. On these pole-and-line cruises, live baitfish were chummed to attract and hold the school close to the vessel. Often, fish will not respond to chumming. Royce

Table 13.4. *Number and percent of fish species associated with 681 bird flocks investigated on pole-and-line cruises in the Hawaiian Islands, 1953–69. Unidentified schools were excluded from this analysis*

Species	Vernacular name	Number of schools	Percentage of schools
Fish			
Katsuwonus pelamis	Skipjack Tuna	514	75.4
Thunnus albacares	Yellowfin Tuna	25	3.7
Euthynnus affinis	Kawakawa	25	3.7
	Mixed tunas	37	5.4
Coryphaena hippurus	Dolphinfish	68	10.0
Mammals			
Delphinidae	Porpoises	12	1.8

& Otsu (1955) and Yuen (1959) reported that fish were caught from only 43 and 47% of the schools chummed, respectively. The high rate of occurrence of Skipjack Tuna under flocks is not surprising. Murphy & Ikehara (1955) found Skipjack Tuna not only the most commonly sighted tuna species in Hawaiian waters, but also the single dominant species in oceanic areas. John J. Naughton (unpublished data) investigated bird flock–fish school interactions in the oceanic waters of the central Pacific and found 73% of identified fish schools to be Skipjack Tuna. Yellowfin Tuna accounted for only 15% of the schools. Naughton suggested that barring various degrees of difficulty in identifying different species, Skipjack Tuna would make up an equally high percentage of the unidentified schools.

Bird flock–fish school interaction is particularly important in Hawaiian commercial fisheries, especially in the Skipjack Tuna pole-and-line fishery. Thus tuna species contribute more than 80%, and Skipjack Tuna more than 65%, of the total catch of ten top-ranked species, which together comprise over 92% of the commercial landing reported to the State of Hawaii (Table 13.5).

Most of the major fisheries in Hawaii have been concentrated in the main Hawaiian Islands. There is, however, increasing interest in extending the various fisheries into the NWHI, where the Hawaiian Islands National Wildlife Refuge protects the breeding grounds of about 5.4 million seabirds

Table 13.5. *Commercial fish landings of the top 10 species for the State of Hawaii, 1961–79*

	Vernacular name	Total landings (MT)	19-year average (MT)
Katsuwonus pelamis	Skipjack Tuna	77394.6	4073.4
Thunnus albacares	Yellowfin Tuna	8257.9	434.6
T. obesus	Bigeye Tuna	5322.7	280.1
Selar crumenophthalmus	Bigeye Scad	5251.7[a]	208.2[a]
Decapterus macarellus	Mackerel Scad	2322.7	122.2
Tetrapterus audax	Striped Marlin	2272.4	119.6
Makaira nigricans	Blue Marlin	1592.8	83.8
Pristipomoides filamentosus	Pink Snapper	1001.0	68.2
Coryphaena hippurus	Dolphinfish	960.6	50.6
Caranx sp.[b]	Jacks	678.2	35.7

[a] Includes the landings for juvenile *Selar crumenophthalmus*. [b] Includes the catches of 11 species of the deep-bodied carangids although *Caranx ignobilis* comprises most of the catch

(Harrison *et al.*, 1983). At present, the fisheries development in the NWHI concerns predominantly benthic stocks, such as lobsters, shrimps and bottom fishes. Although surface trollers have fished for Albacore *Thunnus alalunga*, in waters north of Midway, little effort has focused on other pelagic species. It seems likely that efforts to exploit other pelagic stocks will extend to the waters of the NWHI.

Tern–shearwater feeding guild

Sooty Terns and Wedge-tailed Shearwaters are the most abundant of the 18 species that breed in the NWHI (Harrison *et al.*, 1983). Sooty Terns are by far the most numerous, comprising 48% of the total population; Wedge-tailed Shearwaters comprise 17%. Among the many species of tropical seabirds, terns and shearwaters are also the most frequently associated with schools of tuna and other commercially valuable fishes (King, 1967). Sooty Terns were found 75% of the time and shearwaters 38% within bird flocks on the *Gilbert* pole-and-line cruises. Naughton (NMFS, unpublished data) found that the species composition of bird flocks is most diverse close to islands and that a substantial reduction in the number of species occurs with distance from land.

Because of the strong relationship between the feeding activities of birds and tunas, it is important to determine how much of a dietary overlap exists. Ashmole & Ashmole (1967) examined the food of Yellowfin Tuna captured in surface waters near Christmas Island. They found major differences between the diets of the fish and birds: fish consumed fewer squid and a wider variety of invertebrates. The fish consumed by the tunas also differed significantly from those eaten by birds. They concluded, however, that a large proportion of the items taken by the birds are made available at the surface only by the feeding activities of the tunas. They attributed the difference in the diets mainly to the types of tuna prey that do not come to the surface even when pursued, whereas other organisms such as flyingfish are subject to predation by the birds while escaping the tunas.

Waldron & King (1963) examined 707 stomach samples from Skipjack Tuna in Hawaiian waters, including the Line and Phoenix Islands, and found material representing 11 invertebrate orders and 42 fish families. Fish occurred in 67% of the stomachs and, based on their frequency of occurrence, the highest ranking families were Gempylidae, Scombridae, Mullidae, Chaetodontidae, and Holocentridae in order of importance. Carangids (especially mackerel scad) were important only in the Skipjack Tuna sampled in Hawaii. Crustaceans and squid occurred in 36% and

35% of the stomachs, respectively. Most of the identified squid were ommastrephids. By volume, fish composed 75%, squid 20%, and crustaceans 4% of the Skipjack Tuna food. Scombridae, Carangidae, Mullidae, Nomeidae, and Molidae were the most important fish families. Yuen (1959) found similar results in his study of 573 Hawaiian Skipjack Tuna stomachs. Members of Carangidae (primarily mackerel scad) were by far the most important item in terms of both volume and frequency of occurrence. As in Waldron & King's study, Yuen found nomeids, molids, and scombrids among the highest-ranked fish families. Squid, stomatopods, and decapod crustaceans were also significant contributors to the diet.

By contrast, our study demonstrated that for Sooty Terns, squid (mostly ommastrephids) were the highest-ranked prey items, constituting 53% of the sample volumes (Harrison *et al.*, 1983). Fish accounted for 46% of the volumes; Mullidae, Exocoetidae, Gempylidae, Carangidae (mostly mackerel scad), Nomeidae, and Holocentridae were the highest ranked. Wedge-tailed Shearwaters ate 66% fish, 28% squid, and 1% crustaceans, by volume. Prey items ranked high were the fish species in Mullidae and carangidae (again, mostly mackerel scad) and the squids in Ommastrephidae. Other common prey fish were the monacanthids and exocoetids.

Based on these fish and bird feeding studies, there appears to be a considerable degree of overlap in the diet of Sooty Terns, Wedge-tailed Shearwaters, and Skipjack Tuna. Among the highest-ranking prey items, squid (Ommastrephidae), goatfish (Mullidae), and mackerel scad were very important in all the diets. Other fish belonging to Nomeidae, Gempylidae, and Holocentridae were also commonly taken by both birds and tunas. The higher degree of overlap between Skipjack Tuna and the birds as compared with Yellowfin Tuna and the birds is not surprising. Skipjack Tuna and seabirds are generally surface feeders, and most fish schools found beneath feeding bird flocks are Skipjack Tuna (Table 13.4). Yellowfin Tuna tend to forage at greater depth.

Skipjack Tuna and the seabirds also appear to prey upon organisms of similar sizes. Based on the various Skipjack Tuna feeding studies in the Pacific (Alverson 1963; Waldron & King, 1963; Nakamura, 1965), Blackburn & Laurs (1972) found that the prey of Skipjack Tuna fell mainly in the 10–100 mm size range. In comparison, Harrison *et al.* (1983) found the standard length of Sooty Tern prey items ($n = 326$) to range from 1 to 120mm (mean 48 mm s.d. 19). All of the common prey items, however, were 20–70 mm long. The prey of Wedge-tailed Shearwaters ($n = 212$) ranged from 4 to 145 mm in standard length (mean 57 mm s.d. 25).

To a lesser degree, seabirds also feed in association with schools of Dolphinfish. Unlike Skipjack Tuna, which traverse the water column vertically, Dolphinfish normally remain in the surface waters. This behavior is reflected in the composition of Dolphinfish forage items. In the Pacific, flyingfish and other surface-dwelling species were the dominant prey taken (Tester & Nakamura, 1957; Kojima, 1961; Rothschild, 1964). The size composition of the principal Dolphinfish food organisms is also similar to that taken by the Sooty Terns and Wedge-tailed Shearwaters. Kojima (1961) reported that although the size range of prey was wide, from about 1 to 34 cm, most of the prey were between 2–4 and 10–15 cm.

Future research needs and conclusions

Unlike subpolar and temperate communities, tropical seabird communities have rarely been studied. Research on seabirds is usually restricted to those ecosystems that are faced with major developments such as offshore oil and gas activities or large commercial fisheries. Our recent studies in Hawaii complement the work by Ashmole & Ashmole (1967) at Christmas Island and represent a refinement of many of their ideas concerning diets and trophic relationships among tropical seabirds. However, much work remains for a better understanding of the role of seabirds in tropical and subtropical ecosystems.

Our model that estimates the consumption of prey by the NWHI seabird community would be improved with more precise input parameters. Better population estimates, especially for non-breeding birds, would refine our estimates of prey consumption. In addition, estimates of consumption rates of seabirds could be improved by studies utilizing captive birds in zoos, marine parks, or oceanaria. Most of our current estimates are largely based on theoretical considerations rather than direct measurements.

A major challenge in the study of seabirds in all ecosystems is to improve our understanding of foraging ranges and locations. Speculations concerning foraging locations are too often accepted as fact despite a virtual absence of data. Tropical seabirds range widely in warm waters and, like polar and subpolar species, live many years before breeding. Birds observed feeding at sea are not necessarily breeding birds, nor should they be assumed to be associated with the nearest colony. How far away from colonies birds feed may be inferred from incubation bouts and chicks' feeding frequencies (Harrison & Hida, 1980). However, such indices are very imprecise, and developments in radiotelemetry are necessary to determine feeding locations. In tropical waters, such technological progress would also be of great interest to fishery managers and fishermen. The movements of birds such as Sooty Terns could be used to locate tuna schools efficiently.

Our understanding of the role of marine birds in tropical ecosystems is most limited by our understanding of tropical marine ecology and fisheries. Improvements in our ability to identify juvenile and larval fish and squid in tropical waters will result in refinements in our analysis of dietary specialization among tropical species. In our work in Hawaii (Harrison *et al.*, 1983), we encountered many unidentifiable flyingfish, goatfish, lizardfish and squid, representing many species. For example, 10 goatfish and 9 flyingfish occur in Hawaiian waters (Tinker, 1978). Although there is undoubtedy some theoretical interest in examining feeding overlap using Morisita's Overlap Index (Diamond, 1984), dietary differences among tropical seabird species are masked by our inability consistently to identify prey beyond the family level. Conclusions based on such analyses repeat the unremarkable proposition that tropical seabirds eat much flyingfish and squid. This is roughly equivalent to concluding that Serengeti herbivores have similar diets because they eat various grasses. Because identification of prey is particularly difficult in tropical ecosystems, it is especially important to utilize a multidisciplinary approach to research and to include fishery biologists. Too often dietary studies of seabirds utilize untrained laboratory personnel whose opinions on the identity of half-digested prey are suspect. Improved estimates of available prey must be developed by fishery biologists if projections concerning the impacts of tropical fisheries on seabird communities are to be improved. This is a prerequisite if marine birds are to be used to monitor changes with time in epipelagic marine fauna (Ashmole & Ashmole, 1968). The remarkable Pacific-wide changes during the 1982–83 El Niño event underscore the interest in such studies.

The interaction between seabirds and predatory fish needs careful study. Only about half of the feeding bird flocks observed during the *Gilbert* cruises were confirmed to be associated with predatory fish. Are some seabirds strictly dependent on fish and marine mammals to drive prey to the surface, or are they merely opportunistic? Additional comparisons between the diets of seabirds and predatory fish are needed to clarify differences and similarities in size classes of prey species.

Lastly, the role of tropical seabird colonies in nutrient cycling deserves careful study. The consumption of prey is not a one-way transfer of energy. As much as 30% of the energy ingested by birds is voided as waste (Wiens & Scott, 1975). Birds enrich the waters surrounding their colonies with calories and nutrients (Hutchinson. 1950: 373; Tuck. 1960; Lindeboom. 1984). Ashmole & Ashmole (1967) hypothesized that seabird guano is an important source of nutrients for coral reef communities adjacent to bird colonies. This notion has recently been rejected in certain Canadian waters (Bédard. Therriault & Bérubé. 1980). Careful nearshore measurements of nutrients and estimates on quantities of guano from NWHI seabird colonies should render a realistic assessment of nutrient cycling as it pertains to tropical seabirds.

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Optimal Policies for Rehabilitation of Overexploited Fish Stocks Using a Deterministic Model

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Traditional fisheries models are of limited use during the transitional period when effort is reduced to permit recovery of an overexploited stock. We used a generalized age-structured model to represent stock dynamics during this transitional period and obtained optimal harvesting policies for three overexploited fish stocks using a first-order gradient procedure. The length of the rehabilitation period was affected by (1) the demographic characteristics of the stock, (2) the historical level of exploitation, and (3) the form of the objective function. When a target stock biomass or spawning stock was specified, rehabilitation was relatively rapid due to the sharp initial reduction in fishing effort. Fishing began earlier in the planning horizon when a target harvest was specified; however, stocks recovered more slowly and fishing effort and harvest did not stabilize at the desired levels as rapidly. Policies for maximizing harvest did not usually result in closure of the fishery; however, fishing effort usually exceeded the desired level and sometimes fluctuated considerably from year to year. Our results should aid in the development of rehabilitation policies tailored to specific fisheries or specific management goals.

L'application de modèles traditionnels de pêche est limitée pendant la période de transition quand l'effort est réduit afin de permettre le rétablissement d'un stock surexploité. Les auteurs utilisent un modèle généralisé basé sur l'âge pour représenter la dynamique d'un stock pendant cette période de transition; ils ont ainsi obtenu des plans d'exploitation optimale pour trois stocks surexploités à l'aide de fréquences du premier ordre. La longueur de la période de rétablissement a varié selon les facteurs suivants : 1) les caractéristiques démographiques du stock, 2) le niveau historique d'exploitation et 3) la forme de la fonction objective. La détermination de niveaux cibles pour la biomasse du stock ou le stock reproducteur a permis un rétablissement assez rapide à cause de la forte baisse initiale de l'effort de pêche. Dans le cadre de la planification, la pêche a commencé plus tôt quand on a précisé le niveau cible d'exploitation; toutefois, la récupération des stocks a étré plus lente et l'effort de pêche et les captures ne se sont pas stabilisés aussi rapidement au niveau désiré. En général, les plans de maximalisation des captures n'ont pas entraîné une fermeture de la pêche; toutefois, l'effort de pêche a généralement dépassé le niveau désiré et a parfois varié fortement d'une année à l'autre. Les résultats obtenus devraient servir à l'élaboration de plans de rétablissement adaptés à des pêches précises ou à des buts de gestion déterminés.

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Alverson and Paulik (1973) noted that traditional management models, such as the Beverton–Holt yield-per-recruit model (Ricker 1975), were of limited value for management of developing fisheries because these fisheries typically have not reached steady-state conditions. The same limitation also applies to management of overfished stocks. The latter case is of considerable interest because many stocks are fully exploited or have been overharvested (Cushing 1981). For example, Atlantic menhaden (*Brevoortia tyrannus*) and Pacific ocean perch (*Sebastes alutus*) stocks have been overfished for several years and reductions in fishing effort have been recommended (Schaaf 1979; Archibald et al. 1983; Pacific Fishery Management Council 1984). To facilitate rehabilitation of overexploited stocks, management models are needed to provide quantitative recommendations for the transitional period to lower fishing effort.

Age-structured population models have been used to develop rehabilitation policies for several overexploited fish stocks. For example, Huang and Walters (1983) used an age-structured model to compare short-term approaches for rehabilitation of a large yellow croaker (*Pseudosciaena crocea*) stock. In their study, alternative strategies were selected arbitrarily and compared through simulation studies. Stock rehabilitation required about 15 yr under a constant effort policy, but occurred much more rapidly if the fishery was closed for 3 yr. Ruppert et al. (1985) used an age-structured model to develop optimal rehabilitation policies for the Atlantic menhaden stock. They found that the stock was restored to the optimal steady-state level in about 9 yr using either a constant effort policy or one of four "egg escapement" policies. The steady-state performance of the five policies was somewhat similar, although there were notable differences in harvest during the rehabilitation period. Archibald et al. (1983) compared several constant effort policies for rehabilitation of a Pacific ocean perch stock. Results for a 30-yr planning horizon were used to evaluate the "short-term" performance of these policies; however, simulation runs of 100 yr or more were required to achieve steady-state levels.

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These results demonstrate that the life history characteristics of the stock and the form of the harvesting policy can have important effects on the management strategies employed during the rehabilitation period. Our objective in this study was to examine the effects of planning horizon length, stock demographic characteristics, and objective function type on the form of optimal rehabilitation policies for three overexploited fish stocks. Our results can be used to develop rehabilitation policies tailored to specific fisheries; for example, a policy with gradually decreasing effort levels might be preferable to one that achieves stock rehabilitation quickly.

Methods

Age-structured models have been used to simulate a variety of fisheries, including South African anchovy (*Engraulis capensis*) (Getz 1980, 1985), Atlantic menhaden (Schaaf 1979; Ruppert et al. 1985), Pacific ocean perch (Archibald et al. 1983), large yellow croaker (Huang and Walters 1983), and Arcto-Norwegian cod (*Gadus morhua*) (Walters 1969). The model used in this study was a slightly generalized version of a deterministic model presented by Getz (1980), who assumed that each simulated year consisted of a fishing season followed by a spawning season. We assumed that each year can be divided into a fishing season of length t' and a closed season of length $(1 - t')$. Spawning was assumed to occur either at the beginning of the year or after the fishing season. Following Getz (1980), we assumed that

$$(1)\quad x_{i+1}(k+1) = x_i(k)\exp(-M_i - q_i f(k)t') \qquad (k = 0,\ldots,N-1;\ i = 1,\ldots,\lambda-2)$$

$$(2)\quad x_\lambda(k+1) = x_{\lambda-1}(k)\exp(-M_{\lambda-1} - q_{\lambda-1} f(k)t') + x_\lambda(k)\exp(-M_\lambda - q_\lambda f(k)t')$$

where $x_i(k)$ = number of age i fish in year k, λ = maximum age class used in the model, t' = length of the fishing season, q_i = catchability coefficient for age i fish, M_i = annual instantaneous rate of natural mortality for age i fish, and $f(k)$ = level of fishing effort in year k. The stock–recruitment model was either of the form proposed by Ricker (1975):

$$(3)\quad x_1(k+1) = \alpha\, S(k)\exp(-\beta\, S(k))$$

or Beverton and Holt (1957):

$$(4)\quad x_1(k+1) = 1/(\alpha + \beta/S(k))$$

where α and β were parameters for either the Ricker or Beverton–Holt curve and $S(k)$, the spawning stock in year k, was defined as

$$(5)\quad S(k) = \sum_{i=1}^{\lambda} c_i x_i(k)$$

when spawning occurred at the beginning of the year or

$$(6)\quad S(k) = \sum_{i=1}^{\lambda} c_i x_i(k)\exp(-t'(M_i + q_i f(k)))$$

when spawning occurred after the fishing season, where c_i = fecundity index for age i fish. Harvest in year k was defined as

$$(7)\quad h(k) = \sum_{i=1}^{\lambda} x_i(k) w_i q_i f(k)\,(1 - \exp(-t'(M_i + q_i f(k)))) \div (M_i + q_i f(k))$$

where w_i = weight of age i fish. It should be noted that average weight-at-age may change if optimal and current levels of fishing mortality differ markedly (Ricker 1975). For example, if the mortality rate is reduced under the optimal policy, mean weight-at-age should increase because more fish survive to the larger sizes reached later in the year (Ricker 1975). Density-dependent changes in weight-at-age also might be observed if stock size changes substantially over the planning horizon. These factors may bias long-term estimates of the optimal levels of fishing effort; however, the practical consequences of this result are small if revised estimates of weight-at-age are used to update the policy periodically.

We examined harvesting policies obtained by minimizing

$$(8)\quad \sum_{k=0}^{N-1} (b(k+t') - b^*)^2$$

where b^* represented the target stock biomass at the end of the fishing season and $b(k+t')$ was defined as

$$(9)\quad b(k+t') = \sum_{i=1}^{\lambda} x_i(k) w_i \exp(-t'(M_i + q_i f(k))).$$

To determine the target stock biomass, we assumed that an appropriate level of fishing effort for the rehabilitated stock would be $f_{0.1}$, the level at which the slope of the yield–effort curve was 1/10 the slope of the curve at the origin. This marginal yield criterion frequently has been used in yield per recruit analyses to select an appropriate fishing mortality rate (Sissenwine 1981). This recommended rate of fishing mortality may be considerably lower than the rate needed to obtain maximum sustained yield (MSY), yet the loss in yield may be minor (Sissenwine 1981). In addition to greater economic efficiency (Gulland and Boerma 1973), an additional advantage of this criterion is the maintenance of a larger spawning stock (Sissenwine 1978). Similar advantages should apply when used with yield–effort curves; therefore, we defined b^* as the equilibrium stock biomass obtained at $f_{0.1}$.

The second set of harvesting policies was obtained by minimizing

$$(10)\quad \sum_{k=0}^{N-1} (s(k+t') - s^*)^2$$

where s^* represented the target spawning stock at the end of the fishing season. We defined s^* as the equilibrium spawning stock obtained at $f_{0.1}$ and obtained $s(k+t')$ from (9) by replacing w_i with c_i. Note that $s(k+t')$ is equivalent to $S(k)$ in (6) if spawning occurs after the fishing season.

The third set of harvest policies was obtained by minimizing

$$(11)\quad \sum_{k=0}^{N-1} (h(k) - h^*)^2 + \delta \sum_{i=1}^{\lambda} (x_i(N) - x_i^*)^2$$

where h^* was the equilibrium harvest obtained at $f_{0.1}$, δ was a penalty weight, and $\boldsymbol{x}^*$ (the target number-at-age vector at time N) was defined as the equilibrium number-at-age vector at $f_{0.1}$. Walters (1975) obtained harvesting strategies for Pacific salmon by minimizing

$$(12)\quad \sum_{k=0}^{N-1} (h(k) - h^*)^2$$

and suggested that those strategies conformed more closely to actual management practices than did strategies for harvest maximization. Stock rehabilitation policies that we obtained using (12) were unacceptable, however, for two reasons. First,

TABLE 1. Equilibrium number-at-age vectors obtained at the maximum sustainable level of fishing effort (f_{max}) and twice the level designated as optimal ($f_{0.1}$).

Stock	Historical level of effort	Age class	Number per age class							
Anchovy	f_{max}	1–5+	0.6	0.2	0.0	0.0	0.0			
	2 × $f_{0.1}$		61.5	20.7	6.0	1.6	0.3			
Atlantic menhaden	f_{max}	1–8+	0.6	0.2	0.0	0.0	0.0	0.0	0.0	0.0
	2 × $f_{0.1}$		2.8	1.4	0.3	0.1	0.0	0.0	0.0	0.0
Pacific ocean perch	f_{max}	1–8	28	28	28	28	28	28	27	25
		9–16	24	22	20	18	15	13	11	9
		17–24	8	7	6	5	4	4	3	3
		25–29+	3	2	2	2	13			
	2 × $f_{0.1}$	1–8	118	118	118	118	118	118	111	105
		9–16	99	91	83	75	65	56	48	41
		17–24	35	30	27	24	21	19	17	15
		25–29+	13	11	10	9	70			

any given equilibrium harvest (other than MSY) could be obtained at two different levels of fishing effort (i.e. one above and one below MSY). Stock size was lower at the higher effort level and this was the equilibrium attained by the rebuilding stock. A second problem arose with the use of the scalar quantity h^* as the target harvest from a multi-aged stock. This harvest can be obtained from more than one number-at-age vector, and harvests approximating h^* were sometimes obtained by increasing effort to offset decreases in stock size. We assumed that an appropriate rehabilitation strategy was one leading to a period of stable effort and harvests and incorporated an end point penalty (Getz 1985) into (11) to accomplish this result. Note that policies obtained from (11) or (12) could be inappropriate in some instances because deviations from h^* are treated equally, regardless of direction. Even if stability in harvest is a primary objective, most fishermen and managers would consider harvests larger than h^* to be much less of a problem than harvests smaller than h^*. An alternative approach would be to give less weight to those deviations where harvest exceeds h^*. We did not evaluate that approach but would not expect our results to change substantially because harvests generally would be less than h^* during the rehabilitation period.

The fourth set of harvesting policies was obtained by maximizing

$$(13)\quad \sum_{k=0}^{N-1} h(k) - \delta \sum_{i=1}^{\lambda} (x_i(N) - x_i^*)^2$$

where the end point penalty was used to prevent the stock from being depleted at the end of the planning horizon. A fifth set of harvesting policies was obtained by maximizing Σ log ($h(k)$ + 1), using the same end point penalty as in (13). Ruppert et al. (1985) suggested that a policy for maximizing log (harvest) might be appropriate whenever there is substantial aversion to risk. In our deterministic analysis, however, policies for maximizing harvest and log (harvest) usually were similar; hence, results for the log (harvest) criterion will not be presented herein.

Fishing effort in our analysis was permitted to vary from 0 to f_{max}, where f_{max} was chosen to be the greatest level of fishing effort at which a nonzero equilibrium was attained by the simulated stock. Note that f_{max} also could represent fleet capacity (Ludwig 1981).

We obtained optimal rehabilitation policies by using a first-order gradient procedure (Dyer and McReynolds 1970; Dreyfus and Law 1977; Getz 1985). (A listing or copy of a microcomputer-based version is available from the senior author.) We assumed that the initial state of the system $\boldsymbol{x}(0)$ was known; for example, through application of a stock reconstruction technique such as cohort analysis (Pope 1972). The optimal rehabilitation policy was defined as the N levels of fishing effort $f(0), \ldots, f(N-1)$ that minimized (8), (10), or (11), or that maximized (13), subject to state transformation equations (1)–(6). We obtained the optimal decision sequence by iteratively improving the value of an arbitrary initial sequence $f^0(0), \ldots, f^0(N-1)$ until increases in value were negligible (Dyer and McReynolds 1970; Dreyfus and Law 1977). Changes in the decision sequence were obtained by first expressing the value in year k, $T(k)$, as a recursive formula. For example, the value of a policy for achieving a target harvest was obtained from

$$(14)\quad T(k) = -(h(k) - h^*)^2 + T(k+1) \qquad (k = 0, \ldots, N-1)$$

where $T(N) = -\delta \sum_{i=1}^{\lambda} (x_i(N) - x_i^*)^2$. The gradient vector $\partial T(k)/\partial f(k)$ was computed to determine the direction for changes in the decision sequence. At the jth iteration, the updated decision sequence was obtained as

$$(15)\quad f^j(k) = f^{j-1}(k) + c\,\partial T(k)/\partial f(k)$$

where c was chosen to maximize the increase in value (Dreyfus and Law 1977).

We determined stock rehabilitation policies for a South African anchovy stock, the Atlantic menhaden stock, and a Pacific ocean perch stock (see Hightower and Grossman (1985) and references therein). We obtained rehabilitation strategies for two hypothetical cases by assuming that the historical level of fishing effort was either f_{max} or 2 × $f_{0.1}$ (Table 1). The former case represented a fishery for a heavily overexploited stock, whereas the latter represented a fishery in which the stock was moderately overexploited. In all cases, references to management policies refer to policies for rehabilitation of these hypothetical stocks.

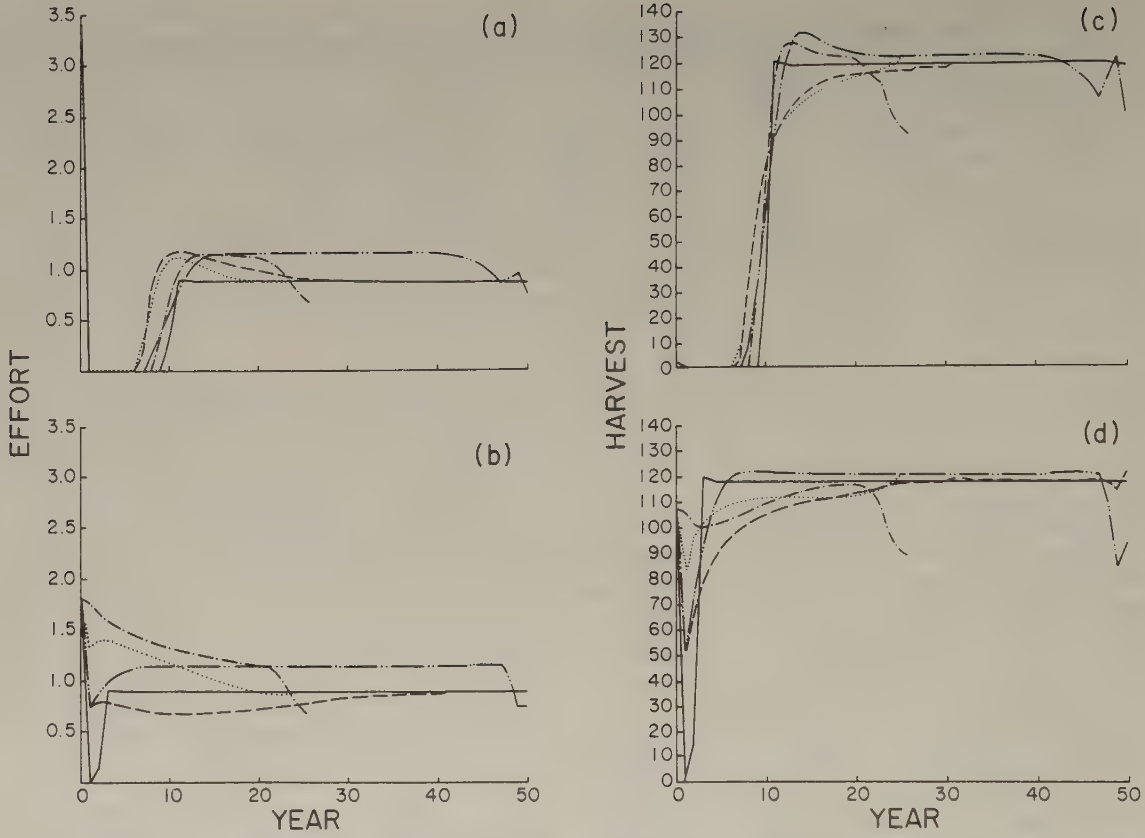

FIG. 1. Optimal levels of fishing effort and harvests for a (a, c) heavily depleted and (b, d) moderately depleted anchovy stock, obtained by maximizing harvest (−·−, 25 yr; −···−, 50 yr), specifying a target spawning stock s^* (—, 50 yr) or specifying a target harvest h^* (···, 25 yr; −−, 50 yr). The 25- and 50-yr policies for attaining s^* differed only in the length of the final constant-effort period, so only the latter policy is shown.

Results and Discussion

Two related problems in developing a policy for stock rehabilitation are (1) determining the length of the rehabilitation period and (2) selecting an appropriate level of annual effort during the rehabilitation period. We found that a planning horizon of two to three times the life span of the fish was sufficient for rehabilitation to occur. Note that these stocks had been fished at the maximum sustainable level, so a shorter rehabilitation period could be used in most instances.

Policies for achieving a target stock biomass and target spawning stock were almost identical for the three stocks examined in this study, so results for a target stock biomass were omitted from Fig. 1−3. Both policies resulted in rapid recovery of the overexploited anchovy and Atlantic menhaden stocks (Fig. 1 and 2). Even when heavily depleted, stocks recovered fully in 5−10 yr and effort was constant during the post-rehabilitation period. A 25-yr planning horizon was sufficiently long for rehabilitation to occur, and increasing the planning horizon to 50 yr merely increased the length of the final constant-effort period. Note that rehabilitation periods were longer for the shorter-lived anchovy stock ($\lambda = 5$) than for the Atlantic menhaden stock ($\lambda = 8$). The difference in the number of age classes is misleading, however, because few Atlantic menhaden lived beyond age 5 unless the level of fishing effort was low. A more important difference between the two stocks is that a Beverton−Holt curve was used to represent the anchovy stock−recruitment relationship, whereas a Ricker curve was used for Atlantic menhaden. This difference enabled the Atlantic menhaden stock to rebuild more quickly because maximum recruitment occurred at an intermediate stock size. For example, in the heavily exploited case, the Atlantic menhaden spawning stock increased to the level producing maximum recruitment in about 4 yr if the fishery was closed. In that same period, the anchovy spawning stock also increased substantially but recruitment produced by that spawning stock was only about one-fifth the maximum level. The Pacific ocean perch stock recovered much more slowly than did the anchovy and Atlantic menhaden stocks; hence, a planning horizon of 100 yr was used. About 60 yr without fishing were needed to rebuild the heavily depleted stock, whereas a 25-yr closure was needed when the stock was only moderately overexploited (Fig. 3). The optimal policy for all three stocks was to close the fishery until stock biomass or spawning stock exceeded the target level. Once the fishery reopened, harvests stabilized at the desired level (h^*) within a few years (Fig. 1−3).

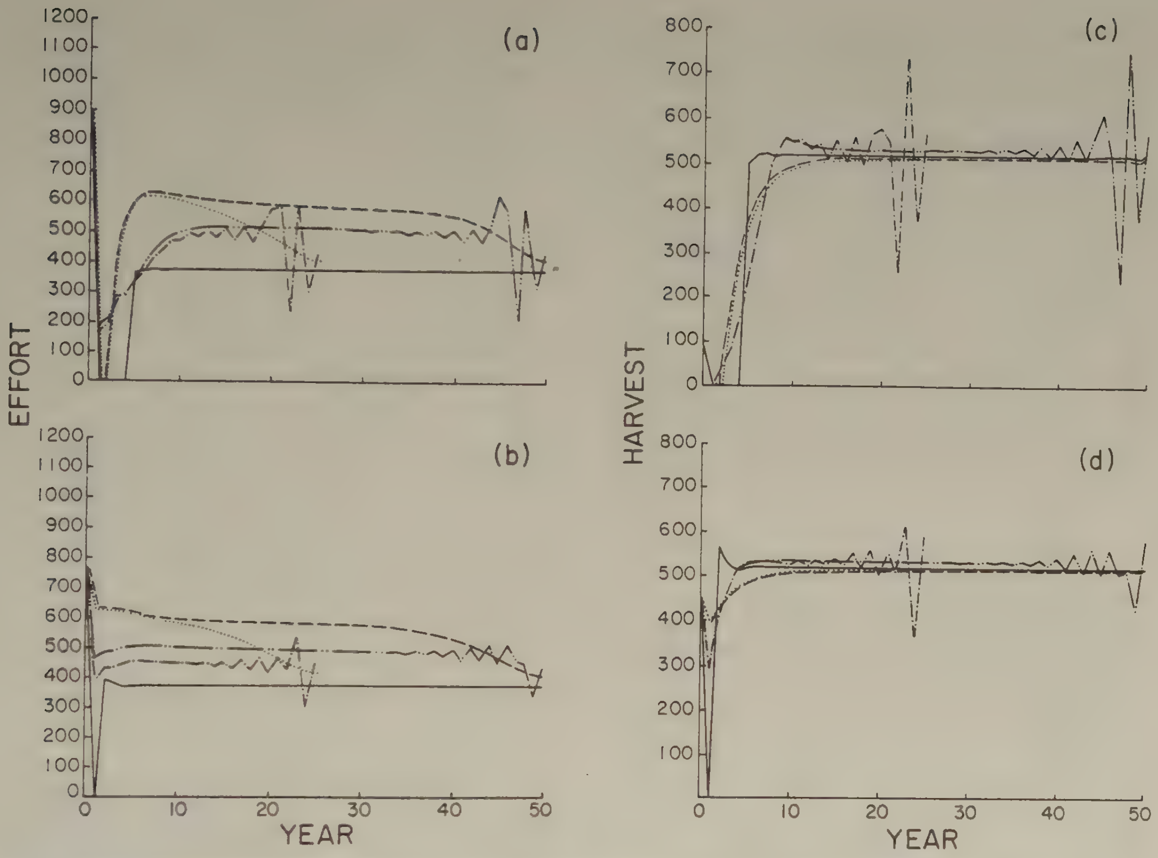

FIG. 2. Optimal levels of fishing effort and harvests for a (a, c) heavily depleted and (b, d) moderately depleted Atlantic menhaden stock, obtained by maximizing harvest (– · –, 25 yr; – · · –, 50 yr), specifying a target spawning stock s^* (—, 50 yr) or specifying a target harvest h^* (· · ·, 25 yr; – –, 50 yr). The 25- and 50-yr policies for attaining s^* differed only in the length of the final constant-effort period, so only the latter policy is shown.

Policies obtained by specifying a target harvest resulted in a more gradual recovery for all three stocks. Fishing began earlier in the planning horizon; however, target levels of fishing effort and harvest were not reached as rapidly (Fig. 1–3). For example, in comparison with results obtained through the use of a target biomass criterion, fishing for the moderately depleted Atlantic menhaden stock began 1 yr earlier, but harvests were lower in years 2–25. One disadvantage of target harvest policies was apparent in cases where the fishery was closed at the start of the planning horizon. Once the fishery was reopened, effort levels increased to above $f_{0.1}$ in order to obtain harvests approximating h^* (Fig. 1–3). Given the difficulty of reducing fishing effort, a more practical approach might be to permit effort to increase only to $f_{0.1}$ and then allow harvest levels to increase gradually to h^*. Policies for attaining a target harvest were affected by a change in the length of the planning horizon. By increasing the time available for convergence to the target vector $\boldsymbol{x}^*$, a more gradual reduction in fishing effort was sometimes possible (Fig. 2).

Policies for maximizing harvest appeared to be the most practical alternative in several of the cases considered herein. For example, the 25-yr policy for the moderately depleted anchovy stock required a gradual reduction in fishing effort to a level of about $f_{0.1}$. For the heavily depleted Atlantic menhaden stock and for both heavily and moderately depleted Pacific ocean perch stocks, harvest maximizing policies were the only management options that did not require closure of the fishery. In addition, harvests at the start of the rehabilitation period were only moderately below the historical level, which is shown in year 0 (Fig. 2d, 3c, 3d). The harvest maximizing policy for the heavily depleted Pacific ocean perch stock might be particularly useful if the species was taken incidentally in other fisheries, because some landings would be permitted throughout the planning horizon. The primary disadvantage of harvest maximizing policies was that, in the anchovy and Atlantic menhaden fisheries, effort frequently increased to the level producing maximum sustained yield (f_{msy}). This occurred in all cases when a 50-yr horizon was used, because convergence to $\boldsymbol{x}^*$ was achieved relatively quickly at the end of the planning horizon. The disadvantage of fishing at f_{msy} is illustrated in Fig. 1 and 2 in that only a slightly higher yield was obtained at a substantially higher effort level. An additional problem with harvest maximizing policies for Atlantic menhaden was that effort sometimes fluctuated substantially from year to year. This phenomenon only occurred near the end of the planning horizon; thus, its practical consequence

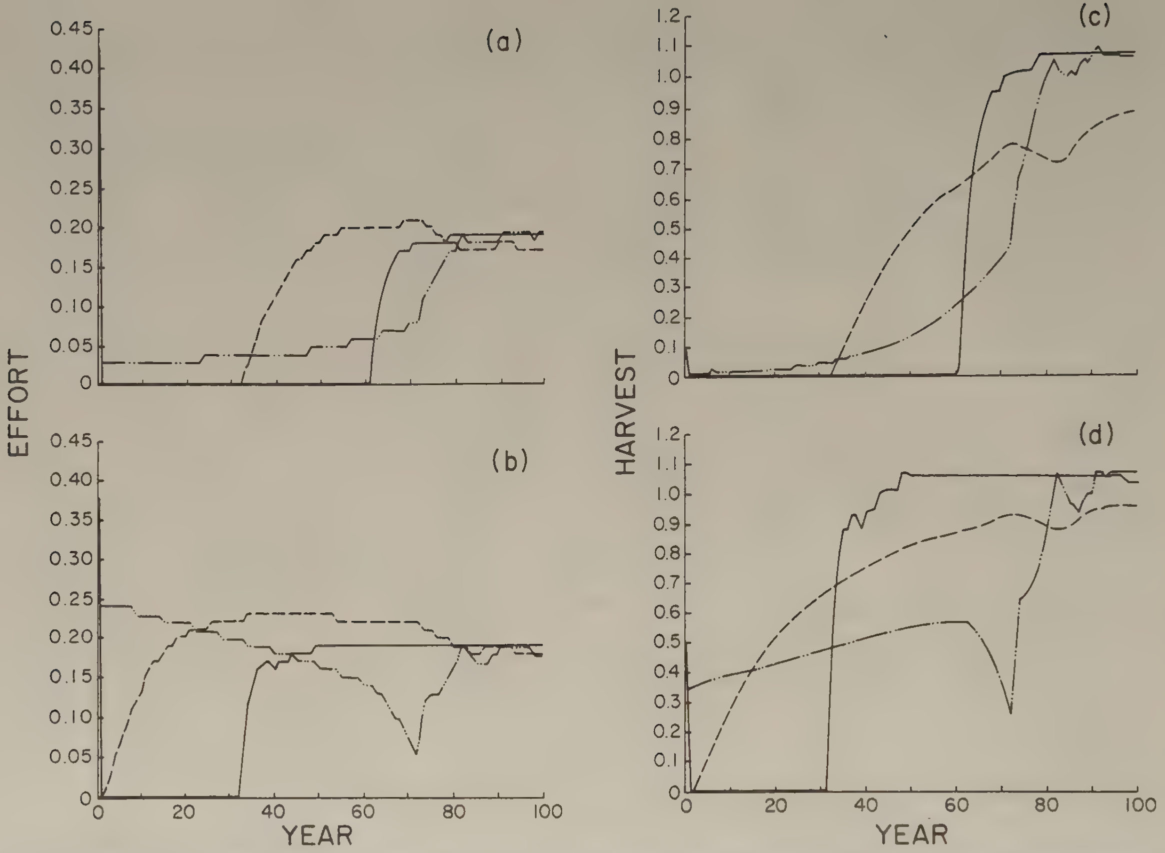

FIG. 3. Optimal levels of fishing effort and harvests for a (a, c) heavily depleted and (b, d) moderately depleted Pacific ocean perch stock, obtained by maximizing harvest (−··−), specifying a target spawning stock s^* (—), or specifying a target harvest h* (−−).

would be negligible if policies were updated regularly.

Variability in recruitment appears to be a significant feature of most commercially important fish stocks (Swartzman et al. 1983); therefore, it is reasonable to question whether the deterministic model used in our analysis is capable of providing useful information to the fishery manager. A stochastic model clearly would be preferable on theoretical grounds; however, in practice, policies obtained from stochastic and deterministic models may be similar because the relative merits of different actions tend to be similar in the two cases (Walters and Hilborn 1978). If a deterministic model is used, a more responsive policy could be obtained by updating the analysis annually. This updated policy would reflect any change in the status of the stock, whether due to random environmental factors or to a change in the level of fishing effort. Another practical advantage of periodic updating is that it can correct errors in previous harvesting policies (Ludwig 1981).

To illustrate this approach, we obtained annually updated policies for achieving a target harvest from the moderately depleted anchovy and Atlantic menhaden stocks (Fig. 4). In each year of a simulated 25-yr period, we obtained an optimal 25-yr rehabilitation policy for the current number-at-age vector $\boldsymbol{x}(k)$. We then used $f(0)$ from the newly determined policy to obtain $\boldsymbol{x}(k + 1)$ from equations (1)−(6). Random variation was introduced by incorporating a multiplicative lognormal error term into the stock−recruitment relationship; consequently, $f(0)$ in year k differed from $f(k)$ obtained in year 0. Thus, each annually updated policy in Fig. 4 represents 25 $f(0)$ values taken from a sequence of 25-yr rehabilitation policies. The two updated policies for the anchovy stock do not differ substantially from the policy obtained in year 0; however, the estimated variance (0.06) of the stock−recruitment relationship for this stock was relatively low (Hightower and Grossman 1985). A more pronounced divergence between original and updated policies can be seen for Atlantic menhaden, for which the estimated variance of the stock−recruitment relationship (0.25) was somewhat greater (Hightower and Grossman 1985). Note that effort decreased sharply when strong year classes entered the Atlantic menhaden fishery (Fig. 4b). These decreases were required to obtain harvests closely approximating h^*. It is unclear, however, whether commercial fishermen would be willing to forego increased harvests and accept fluctuations in effort merely to reduce variability in annual harvest. From the manager's viewpoint, the policy obtained in year 0 may be preferred in that changes in fishing effort are more gradual and known in advance; thus, implementation of a given policy would be simpler from both a practical and political standpoint. Finally, it should be noted that information regarding stock condition generally is available only after a lag of several years; hence, annual updates of

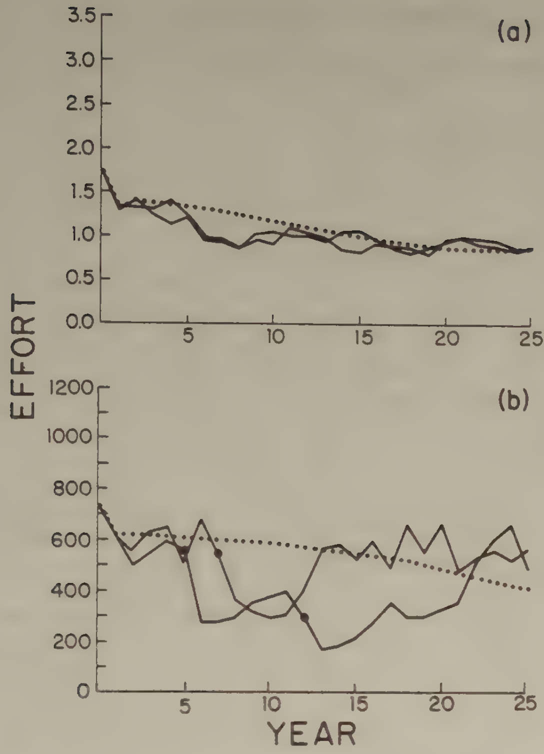

FIG. 4. Optimal (···) and annually updated (—) harvesting policies for moderately depleted (a) anchovy and (b) Atlantic menhaden stocks. For each stock, the three policies were obtained by specifying a target harvest h^*; updated policies were obtained for two simulated 25-yr periods. Closed circles denote years in which a strong year class entered the simulated Atlantic menhaden fishery.

the rehabilitation policy may not be practical.

In cases where variability in recruitment is high and periodic updating is not possible, a stochastic model may be essential. Once a random component is introduced, however, it is no longer meaningful to estimate optimal effort levels for each year of the planning horizon. A better approach would be to develop a stationary policy, where harvest depends only on stock size and not on the number of years remaining in the planning horizon (Ruppert et al. 1985). A stationary policy might have only one (constant effort) or two (egg escapement) parameters (Ruppert et al. 1985) instead of the 25–100 parameters (effort levels) used in our deterministic analysis.

The only obvious disadvantage of using a stochastic model is that much greater computational effort is required to obtain and evaluate optimal policies. An important advantage is that the model can be used to evaluate probabilistic questions that cannot be addressed with a deterministic model. For example, alternative policies could be compared using criteria such as variability in annual harvest (Ruppert et al. 1985), or the probability of full recovery (Overholtz et al. 1986) or of further declines in stock size (Archibald et al. 1983) during the planning horizon. In addition, the probability of stock depletion could be considered explicitly when developing a harvesting policy if a stochastic model was used (Swartzman et al. 1983). The deterministic approach used in this study might play a complementary role in situations where a stochastic model is required by providing insights into the expected behavior of the stock during the rehabilitation period.

In practice, any management plan represents a compromise between user groups with conflicting objectives. These user groups may have widely divergent views regarding the appropriateness of restrictions on fishing effort or of the proper balance between short- and long-term benefits. Consequently, optimization studies might best be viewed as a means to explore and compare policies obtained through the use of alternative management objectives (Peterman et al. 1978). For example, alternative policies for achieving a target harvest can be obtained by varying the length of the planning horizon. A longer planning horizon could be chosen for a stock rehabilitation plan so that changes in the level of fishing effort would be more gradual. As Gunderson (1984) illustrated, management policies requiring rapid changes in either effort or catch levels are difficult to implement. Hence, longer-term planning may be necessary, so that fishermen can attempt to offset reductions in catch by redirecting effort toward less heavily exploited stocks.

Conclusions

Our results for these hypothetical fisheries were, in a general sense, predictable in that an increase in life span or degree of prior exploitation increased the time required for rehabilitation. It appears that rehabilitation will be particularly difficult for long-lived fishes such as Pacific ocean perch, because changes in stock size will be slow and could be masked by variability in recruitment or by errors in the stock assessment. Our results also suggested that the form of the underlying stock–recruitment relationship could affect the rate of rebuilding, in that rehabilitation might be slower if recruitment increased asymptotically than if maximum recruitment occurred at an intermediate stock size. Rehabilitation would also be difficult for stocks with the type of stock–recruitment relationship Overholtz et al. (1986) reported for Georges Bank haddock (*Melanogrammus aeglefinus*). They found that, although recruitment was quite variable, poorer year classes were observed in years when spawning biomass was less than a critical minimum size. In such cases, rebuilding would be particularly slow until the critical minimum size was exceeded.

Although the form of the objective function affected both the rate at which rebuilding occurred and the patterns of annual effort and harvest, mean annual harvest was quite similar for the four cases we considered (Table 2). This suggests that alternative optimal policies might be compared using other criteria, such as the number of years without fishing, or the magnitude of year-to-year changes in effort or harvest. We found that variability in harvest was lowest for the target harvest policy and highest for the target spawning stock and stock biomass policies (Table 2). Variability was high for the latter policies because the fishery remained closed until stock size rebuilt to the target level. Therefore, the best use of those policies may be in determining the minimum time required for full rehabilitation, or alternatively, the maximum time that the fishery should remain closed. Those policies could be practical alternatives in some cases, however, if effort could be diverted to other fisheries during the rehabilitation period. Policies for attaining a target harvest should be somewhat less extreme, although closure might still be optimal for heavily depleted stocks. Closing such a fishery might be a feasible management option, however, because the equilibrium harvest from a

TABLE 2. Mean harvest and coefficient of variation (in parentheses) obtained for each of four objective functions (t = metric tons).

Stock	Historical level of fishing effort	Length of planning horizon (yr)	Objective: Maximize harvest (1000 t)	Target spawning stock (1000 t)	Target stock biomass (1000 t)	Target harvest (1000 t)
Anchovy	f_{max}	25	74.4 (75)	72.7 (80)	72.9 (79)	72.6 (68)
		50	97.9 (47)	95.7 (49)	95.8 (49)	95.7 (43)
	$2 \times f_{0.1}$	25	108.8 (7)	109.8 (28)	109.9 (28)	110.2 (7)
		50	116.9 (12)	114.2 (19)	114.3 (19)	111.1 (13)
Atlantic menhaden	f_{max}	25	433.8 (44)	435.9 (45)	435.9 (45)	427.6 (36)
		50	483.0 (30)	477.7 (30)	477.7 (30)	473.9 (25)
	$2 \times f_{0.1}$	25	513.3 (13)	500.6 (21)	500.5 (21)	500.8 (6)
		50	522.2 (7)	510.0 (14)	510.0 (14)	510.6 (4)
Pacific ocean perch	f_{max}	100	0.4 (113)	0.4 (127)	0.4 (129)	0.4 (82)
	$2 \times f_{0.1}$	100	0.6 (39)	0.7 (68)	0.7 (69)	0.7 (35)

heavily depleted stock may be small (Fig. 1c, 2c, and 3c). If alternative fisheries are not available, policies for maximizing harvest may be more appropriate in that closure would rarely be optimal.

Another approach that would yield less drastic changes in effort would be to rebuild the stock in stages, beginning with a lower target stock biomass or spawning stock. For example, b^* could be the equilibrium stock biomass at f_{msy}, so it would be reached more quickly than the larger stock at $f_{0.1}$. It is likely, however, that no single objective function will provide a directly implementable harvesting policy. Nevertheless, our approach still provides a means of exploring the effects of various management options on stock dynamics and of comparing alternative policies that might be combined into a workable suboptimal policy.

Acknowledgments

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Status of the widow rockfish fishery

Prepared by: Joseph E. Hightower and William H. Lenarz

Abstract

Cohort and catch-at-age analysis were used to estimate fishing mortality rates and population size for widow rockfish (Sebastes entomelas), using 1980-1986 catch-at-age data. Fishing mortality was moderately higher in 1986 than in 1985, due to a decrease in stock size and an increase in harvest. Projected stock biomass in 1987 and 1988 should be slightly lower than the estimated levels in 1985 and 1986. Using results from cohort analysis, estimates of MSY ranged from 7,700 to 12,000 metric tons (mt), with an average of 10,100 mt. The recommended fishing mortality rate for fully recruited fish was 0.30. At this level of fishing effort, average yield in 1988 and 1989 (an estimate of ABC) would be 12,500 mt. Using results of catch-at-age analysis, estimates of MSY ranged from 7,800 to 12,200 mt, with an average of 10,200 mt. At a recommended fishing mortality rate of 0.30 for fully recruited fish, average yield in 1988 and 1989 would be 11,700 mt. Because each of the two stock reconstruction techniques has advantages and disadvantages, we recommend calculating ABC as the average of the two ABC estimates. This combined estimate of the 1988 ABC is 12,100 mt.

Introduction

This report represents an update of the widow rockfish (Sebastes entomelas) status report submitted in August 1986 (Hightower and Lenarz 1986). Included is (1) a review of the 1986 report and of recent events in the fishery, (2) estimates of the current status of the stock, (3) and recommendations for harvest in 1988.

Summary of previous assessment

The estimate of acceptable biological catch (ABC) for 1987 was 12,400 metric tons (mt), an increase of 3,100 mt over the 1986 ABC. The increase was due in part to an increase in estimated mean recruitment, but primarily to an upward revision in the estimated size of the 1978-1980 year classes. Estimates of total stock biomass and spawning biomass were relatively stable from 1984 through 1987.

Recent History of the fishery

Landings in 1986 were slightly higher than in 1985, due primarily to increased landings in the northern part of the Columbia INPFC area (Table 1, Figure 1). As in earlier years, the change in landings should not be attributed to a change in stock size, but rather to the difficulty of using regulations to remove OY exactly. The fishery proceded at a somewhat slower pace in 1986 than in 1985, due in part to good fishing for pink shrimp (Pandalus jordani).

The 1980 year class dominated the catch numerically in 1986, although as in earlier years, the 1977-1979 year classes were also an important component (Table 2, Figure 2). Also as in earlier years, a large percentage of the 1986 catch (71 percent by number) was comprised of fish less than age 9, the age at full maturity (Figure 3). A shift in the age distribution toward older fish is likely as the 1977-1980 year classes move through the fishery. As of 1986, peak catches have occurred for all year classes through 1978.

The OY for 1987 was set at 12,500 mt, which was the October 1986 estimate of ABC. The original estimate of 12,400 mt (Hightower and

Table 1. Landings (metric tons) of widow rockfish by area and year from 1979 through 1986.

Area	1979	1980	1981	1982	1983	1984	1985	1986
INPFC Vancouver	329	143	1,991	3,969	1,596	594	446	557
Northern Columbia	432	9,426	7,969	4,625	2,490	2,086	2,128	3,508
Nelson Island	1,680	3,192	2,056	489	0	0	0	0
Newport Deeps	0	0	272	4,953	1,337	2,147	1,688	1,983
Heceta-Coq.	214	2,589	9,973	1,487	792	1,600	1,305	679
Southern Col.	1,894	5,781	12,301	6,929	2,129	3,747	2,993	2,662
INPFC Columbia	2,326	15,207	20,270	11,554	4,619	5,833	5,120	6,170
INPFC Eureka	2,166	4,736	3,430	3,993	2,442	2,256	2,313	1,632
INPFC Monterey -Conception	120	304	2,000	6,997	1,554	988	977	971
Total	4,941	20,390	27,691	26,513	10,211	9,671	8,856	9,329

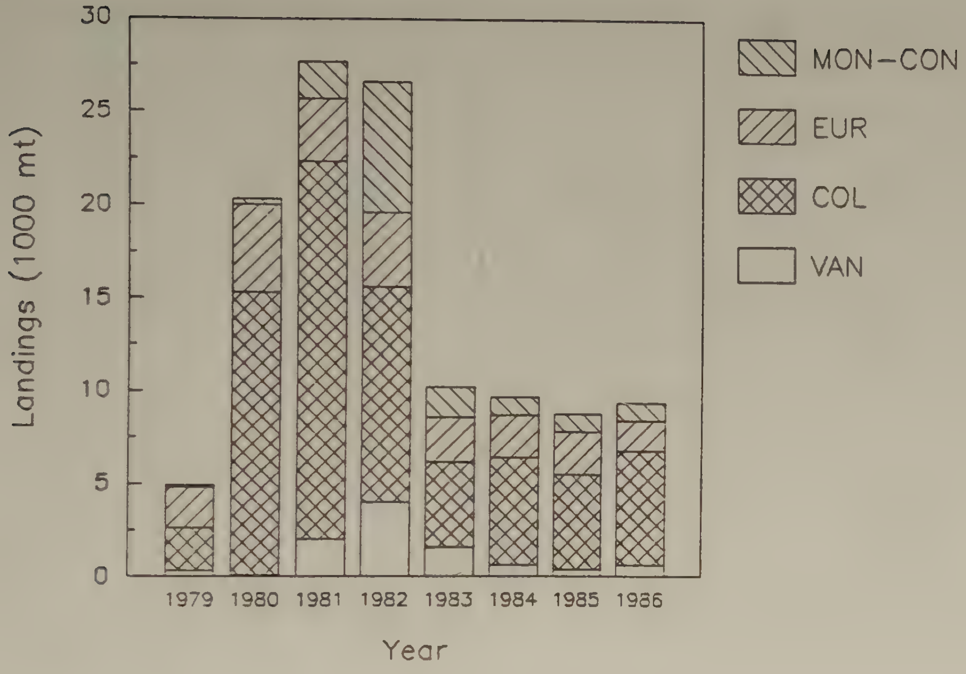

Figure 1. Landings of widow rockfish by INPFC area from 1979 through 1986.

Table 2. Estimates of the number of widow rockfish landed by year class (millions) from 1980 through 1986.

Year Class	1980	1981	1982	1983	1984	1985	1986
65+	1.856	1.409	2.945	1.357	0.810	0.473	0.504
66	0.567	0.579	0.826	0.191	0.116	0.062	0.056
67	0.855	0.853	1.093	0.279	0.144	0.073	0.060
68	1.675	1.356	1.403	0.365	0.237	0.093	0.076
69	2.237	2.194	1.647	0.364	0.338	0.067	0.070
70	5.590	5.633	3.849	0.690	0.744	0.400	0.317
71	3.580	5.130	1.960	0.391	0.392	0.173	0.064
72	0.904	1.483	0.727	0.222	0.102	0.047	0.017
73	0.460	0.885	0.933	0.272	0.170	0.037	0.037
74	0.454	1.626	1.513	0.322	0.189	0.148	0.162
75	0.300	2.219	1.924	0.620	0.471	0.268	0.243
76	0.001	0.690	1.512	0.705	0.576	0.292	0.166
77	0.000	0.899	2.599	2.484	3.046	1.801	1.318
78		0.000	0.510	2.272	3.338	3.786	2.259
79			0.015	0.334	0.516	1.402	1.644
80				0.015	0.026	0.920	2.827
81					0.002	0.053	0.656
82						0.001	0.022
83							0.000

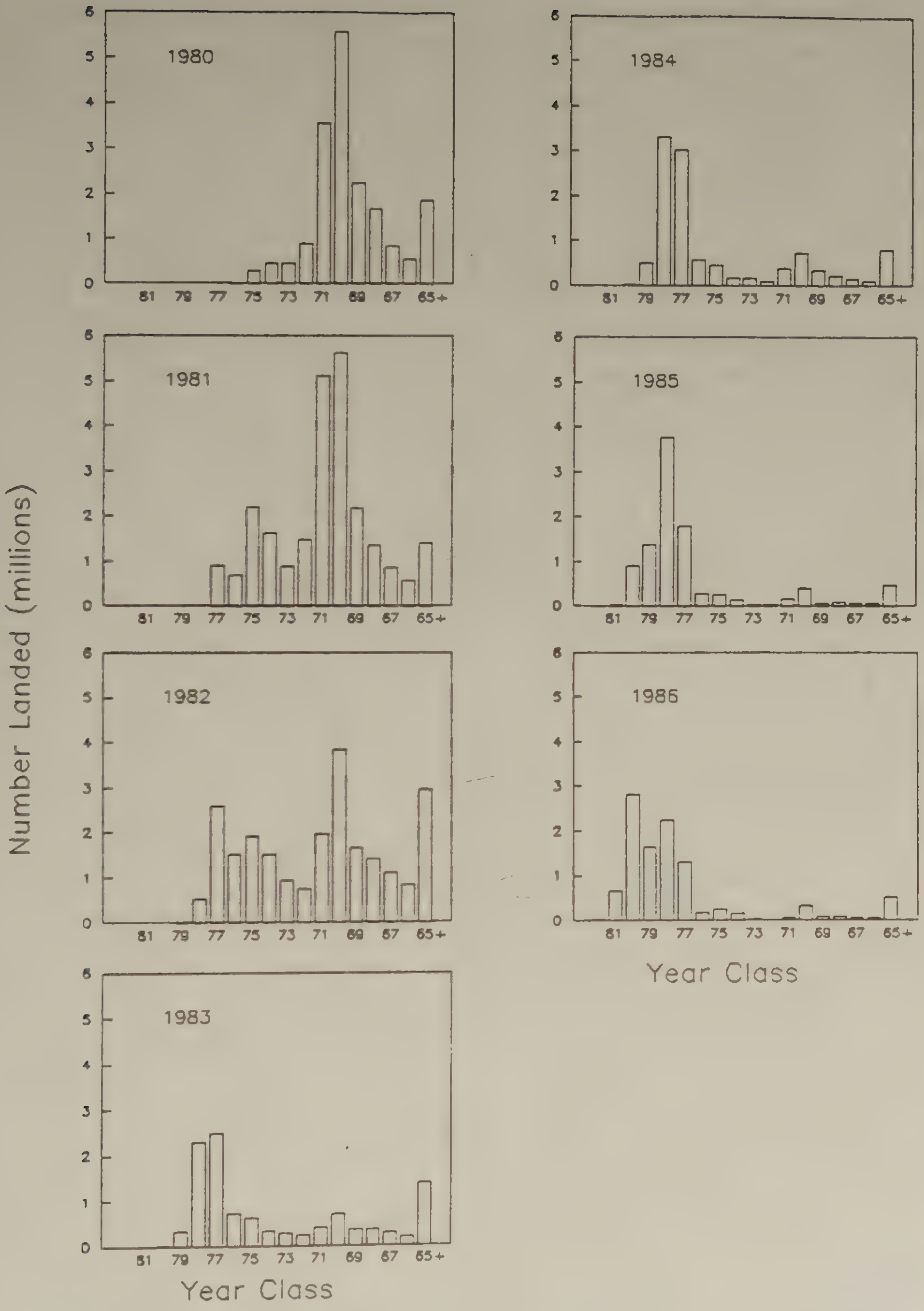

Figure 2. Total numbers of widow rockfish from each cohort in Washington, Oregon, and California landings from 1980 through 1986.

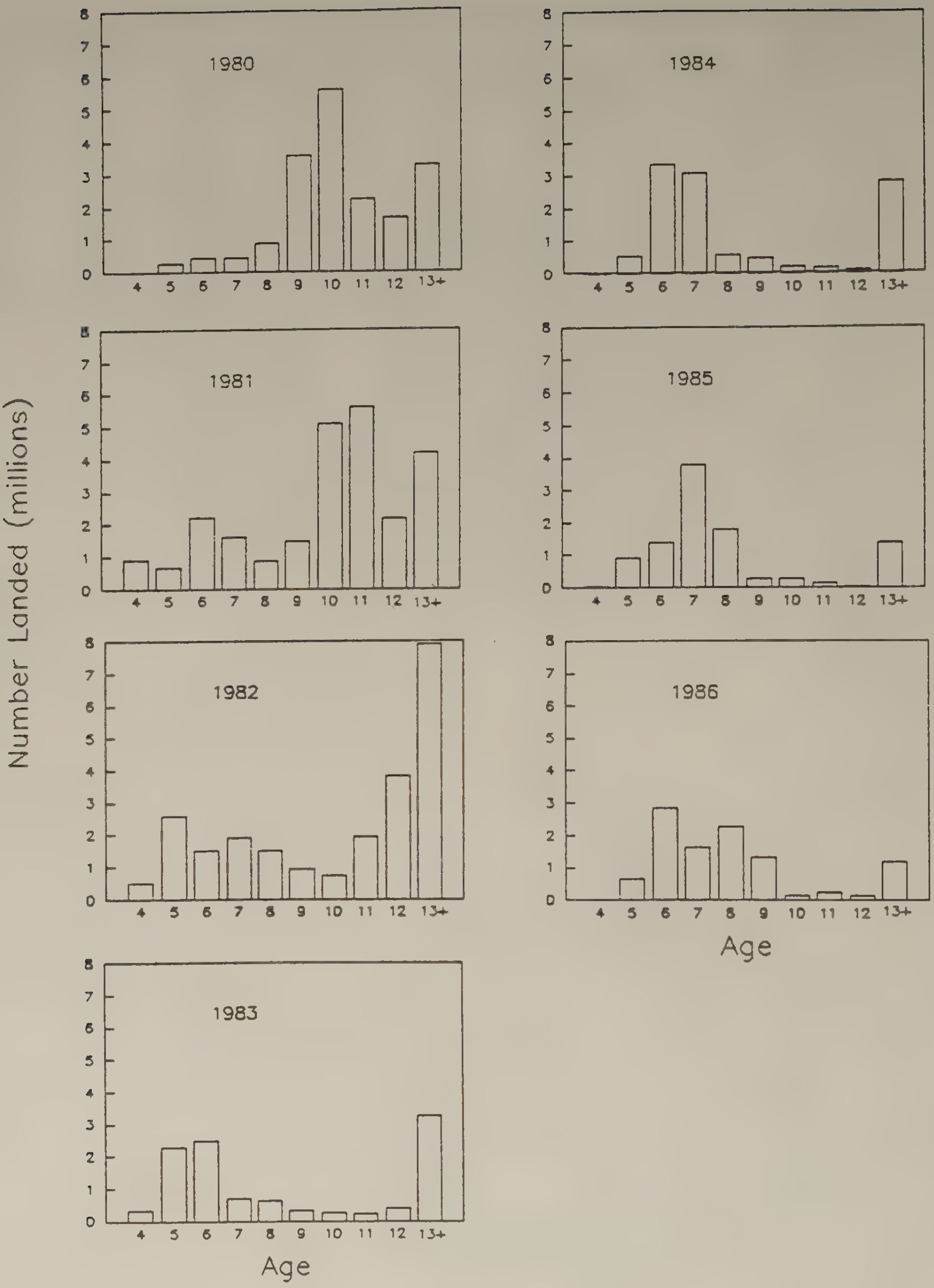

Figure 3. Total numbers of widow rockfish from each age group in Washington, Oregon, and California landings from 1980 through 1986.

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Lenarz 1986) was based on projected 1986 landings of 9,600 mt. In response to a Council request, a revised estimate of ABC (12,500 mt) was obtained by using an updated forecast that 1986 landings would be about 9,300 mt. Preliminary estimates are that 1987 landings will be about 12,500 mt, and that the OY will be reached by October or November.

Assessment Methodology

The same approaches and assumptions used in the 1986 assessment were used in this assessment. All analyses were done using two levels for the instantaneous rate of natural mortality (M). These assumed rates were based on a catch curve analysis, and were thought to be approximate lower (0.15) and upper (0.20) bounds for M.

Cohort analysis (Murphy 1965) and catch-at-age analysis (Deriso et al. 1985) were used to estimate instantaneous rates of fishing mortality (F) and population size (N, in numbers of fish). By comparing the more traditional approach (cohort analysis) to the more recently developed approach using nonlinear least squares (catch-at-age analysis), we were able to determine whether our results were sensitive to the assumptions or methods used in either analysis.

As in the 1986 assessment, cohort analysis was done by linking adjacent cohorts, under the assumption that F was equal for 9- and 10-year-old fish in a given year. For the 1970 through 1977 cohorts, we used the same starting value used in the 1985 and 1986 assessments ($F_9(1984)$). This starting value assessment was originally selected by varying $F_9(1984)$ until we produced a decline in average F of about 50 percent from 1982 to 1983 and about 10 percent from 1983 to 1984. Starting F values for cohorts younger than 1977 were obtained by assuming that the ratio of F for ages less than 9 to age 9 was the same in 1986 as in earlier years. For example, the estimate of $F_8(1986)$ was obtained by multiplying $F_9(1986)$ by $\bar{F}_8/\bar{F}_9$, where $\bar{F}_8$ and $\bar{F}_9$ were averages for years 1980-1985. Starting F values for cohorts older than 1970 were obtained by using the same ratio method, except that estimates of mean F were obtained for the years 1981-1986. As in earlier assessments, the microcomputer program GENCOH was used for the cohort analysis.

The catch-at-age analysis was done using CAGEAN, a microcomputer program developed for use with Pacific halibut (Deriso et al. 1985). The approach differs from cohort analysis in several ways. The most important difference is that fishing mortality is assumed to be separable into a product of an age-specific selectivity coefficient s_a and a full-recruitment fishing mortality rate F(k):

$$F_a(k) = s_a\ F(k)$$

where $F_a(k)$ is the fishing mortality rate for age-a fish in year k and $s_a = 1$ for at least one age. The separability assumption is important because it reduces the number of unknown fishing mortality parameters from 63 (7 years X 9 ages) to 15 (7 fishing mortality rates plus 8 selectivity estimates (with s_{10} assumed to be 1)).

Several studies have noted that catch-at-age data are insufficient to estimate stock abundance reliably, because estimates of F and N have a large negative correlation (see Deriso et al. 1985). To stabilize parameter estimates, one of two types of auxilliary information can be used: additional information about model parameters or additional assumptions about stock dynamics (Deriso et al. 1985). For our catch-at-age analysis, we used the same assumptions about relative changes in F from year to year that were used to determine appropriate starting Fs for cohort analysis. These assumptions were incorporated into the catch-at-age analysis by using average Fs from cohort analysis as a relative measure of fishing effort (the annual averages shown in Table 3). A model parameter (lambda) adjusts the amount of influence given to the "effort" data. If lambda=0, no relationship between F and effort is assumed. If lambda=1000, the relationship between F and effort is essentially exact (Deriso et al. 1985). Results from catch-at-age analyses of Pacific halibut data were similar for lambda values of 0.1 to 1.0 (Deriso et al. 1985), and production runs are done using the value 0.5 (P. R. Neal, unpublished documentation of CAGEAN program). In our 1986 assessment, we obtained very similar results using lambda values of 0.1 to 10.0; therefore, the 1987 analysis was done using only the lambda value 0.5. The only change in methodology for this assessment was that fish ages 13 and older were included as an additional pooled age group.

We used the same age-structured simulation model used in earlier assessments and made the following assumptions regarding recruitment into the fishery:

1) For the low recruitment case, we assumed that the 1982 year class was equal in size to the average of the lower 50% of all recruitment estimates (R_{low}). The size of the 1983 year class was assumed to be 0, based on a juvenile rockfish survey indicating very poor spawning success off the central California coast. Recruitment of subsequent year classes was assumed to be equal to $\bar{R}$, the average for the 1968 to 1981 cohorts.
2) For the high recruitment case, recruitment was assumed to be equal to R_{low} in 1983 and otherwise equal to $\bar{R}$.
3) For the density-dependent case, recruitment was assumed to be determined by a Beverton-Holt relationship. The parameters were obtained by assuming that recruitment would be reduced by 10 percent if spawning stock was reduced to 50 percent of the unfished level ($R_{0.5}/R_{1.0}=0.90$). Spawning stock estimates were obtained from the stock reconstruction analyses.

Number-at-age vectors at the start of 1988 were obtained as follows. The two stock reconstruction techniques provided estimates of the number-at-age vector at the beginning of 1986. Estimates of F-at-age in 1986 were used to project the number of fish ages 6 through 13+ present at the start of 1987. Recruitment in 1987 was obtained using the above assumptions about the strength of the 1982 year class. We then solved iteratively for the fishing mortality rates needed to obtain a 1987 harvest of 12,500 mt, using a selectivity curve obtained from the mean F-at-age vector (cohort analysis) or the least squares fit (catch-at-age analysis). Recruitment in 1988 was obtained using the above assumptions about the strength of the 1983 year class.

We used two approaches to develop harvest recommendations for 1988. The first approach was to maintain F at the level estimated to produce maximum sustained yield (MSY). The second approach was to maintain yield at a constant level.

Results

Estimates of age-specific Fs for 1980-1985 from cohort and catch-at-age analysis (Tables 3 and 4) were quite similar to the results presented in the 1986 assessment. Preliminary indications are that F increased in 1986, not only because harvest was higher, but also because stock size decreased from 1985 to 1986. The decrease in stock size can be attributed in part to the declining abundance of the strong 1977 and 1978 year classes (Tables 5 and 6), which is only partially offset by the recruitment of the strong 1980 year class. The primary reason, however, for the sharp reduction in biomass indicated by cohort analysis is the substantially lower estimate of the number of fish ages 13 and older (Table 5). Although this may be an artifact of the method used to estimate N_{13+} (see below), both approaches indicate a decline from 1985 to 1986, with a gradual further decline predicted through 1988 (Table 7). For the years 1980 through 1987, estimates of stock biomass and spawning stock (for ages 5+) were generally quite similar to estimates from the 1986 assessment (Table 7). At the start of 1986, stock biomass and spawning stock were about 55 and 35 percent, respectively, of the estimated levels in 1980.

Estimates of recruitment at age 5 were generally similar to estimates from the 1986 assessment, except that result of both stock reconstruction techniques indicated that the strength of the 1980 year class was underestimated in the 1986 report (Figure 4). Based on cohort analysis, average recruitment was about 25.5 and 32.5 million age-5 fish for $M=0.15$ and 0.20, respectively. Estimates of average recruitment from catch-at-age analysis were 26.1 and 33.4 million age-5 fish for $M=0.15$ and $M=0.20$, respectively.

Estimated selectivity patterns from cohort and catch-at-age analysis were similar for fish ages 5-11 (Figure 5). The pattern derived from catch-at-age analysis indicates sharply lower vulnerability for fish ages 12 and older. A similar result was obtained from cohort analysis in the 1986 assessment. The current cohort analysis predicts only slightly reduced vulnerability for older fish, due apparently to the relatively large estimated landings in 1986 of 11- and 12-year-old fish (Table 2). The 1986 catch of age-12 fish had a particularly great impact on the results because the starting value for the entire analysis is for the same cohort. Because $F_{10}(1984)$ (and therefore $N_{10}(1984)$) is fixed, a large catch from that cohort two years later is attributed to a high rate of fishing mortality. The unusually high $F_{12}(1986)$ produces a low estimate of $N_{13+}(1986)$, because N_{13+} is estimated as C_{13+}/u_{12} under the assumption that the exploitation rate is equal for fish ages 12 and older. As mentioned earlier, the low estimate for $N_{13+}(1986)$ causes 1986 biomass and spawning stock estimates from cohort analysis to drop sharply (Table 7).

Estimates from catch-at-age analysis were less effected by the 1986 catch of older fish because of the structure imposed by the constant selectivity assumption. The disadvantage is that if a change in fishing patterns occurred in 1986, it would not be accurately represented by the catch-at-age analysis. The model can be fitted to catch data from two or more periods where selectivity patterns differed. That assumption was not used here, however, because the high catch of

Table 3. Estimates of F for widow rockfish by age and year obtained by cohort analysis.

M=0.15

Age	1980	1981	1982	1983	1984	1985	1986	Ave
5	0.030	0.102	0.097	0.063	0.025	0.022	0.027	0.052
6	0.073	0.297	0.318	0.120	0.119	0.082	0.081	0.156
7	0.108	0.379	0.428	0.227	0.200	0.182	0.123	0.235
8	0.201	0.295	0.686	0.224	0.277	0.165	0.149	0.285
9	0.227	0.551	0.542	0.281	0.250	0.208	0.166	0.318
10	0.227	0.551	0.542	0.281	0.250	0.208	0.166	0.318
11	0.215	0.355	0.396	0.296	0.268	0.298	0.279	0.301
12	0.195	0.319	0.412	0.120	0.203	0.082	0.584	0.274
Ave	0.160	0.356	0.428	0.202	0.199	0.156	0.197	

M=0.20

Age	1980	1981	1982	1983	1984	1985	1986	Ave
5	0.026	0.091	0.089	0.061	0.025	0.023	0.030	0.049
6	0.066	0.270	0.294	0.115	0.120	0.087	0.092	0.149
7	0.096	0.350	0.398	0.217	0.201	0.193	0.140	0.228
8	0.182	0.270	0.643	0.214	0.277	0.175	0.169	0.276
9	0.206	0.509	0.506	0.269	0.250	0.220	0.188	0.307
10	0.206	0.509	0.506	0.269	0.250	0.220	0.188	0.307
11	0.200	0.330	0.371	0.283	0.268	0.316	0.318	0.298
12	0.190	0.307	0.395	0.117	0.203	0.086	0.685	0.283
Ave	0.146	0.330	0.400	0.193	0.199	0.165	0.226	

Table 4. Estimates of F for widow rockfish by age and year, obtained by catch-at-age analysis with lambda=0.5.

M=0.15

Age	1980	1981	1982	1983	1984	1985	1986	Ave
5	0.035	0.080	0.101	0.046	0.041	0.033	0.038	0.053
6	0.100	0.227	0.286	0.131	0.115	0.093	0.108	0.151
7	0.147	0.336	0.423	0.194	0.170	0.138	0.159	0.224
8	0.161	0.368	0.463	0.213	0.187	0.151	0.175	0.245
9	0.189	0.431	0.543	0.250	0.219	0.178	0.205	0.288
10	0.185	0.421	0.531	0.244	0.214	0.173	0.200	0.281
11	0.180	0.410	0.517	0.237	0.208	0.169	0.195	0.274
12	0.125	0.285	0.359	0.165	0.145	0.117	0.135	0.190
13+	0.082	0.187	0.235	0.108	0.095	0.077	0.089	0.125
Ave	0.134	0.305	0.384	0.177	0.155	0.126	0.145	

M=0.20

Age	1980	1981	1982	1983	1984	1985	1986	Ave
5	0.031	0.072	0.093	0.044	0.041	0.035	0.043	0.051
6	0.088	0.206	0.266	0.126	0.116	0.099	0.122	0.146
7	0.132	0.307	0.395	0.188	0.172	0.148	0.182	0.218
8	0.145	0.338	0.435	0.206	0.190	0.163	0.200	0.240
9	0.170	0.396	0.509	0.242	0.222	0.191	0.235	0.281
10	0.165	0.386	0.497	0.236	0.217	0.186	0.229	0.274
11	0.160	0.374	0.481	0.229	0.210	0.180	0.222	0.265
12	0.112	0.261	0.336	0.159	0.147	0.126	0.155	0.185
13+	0.080	0.186	0.240	0.114	0.105	0.090	0.111	0.132
Ave	0.120	0.281	0.361	0.172	0.158	0.135	0.166	

Table 5. Estimates of population size (millions of fish) of widow rockfish by age and year, obtained by cohort analysis.

M=0.15

Age	1980	1981	1982	1983	1984	1985	1986
5	11.1	7.7	30.2	39.6	22.9	46.4	26.5
6	6.9	9.3	5.9	23.6	32.0	19.2	39.1
7	4.8	5.5	5.9	3.7	18.0	24.4	15.3
8	5.3	3.7	3.3	3.3	2.6	12.7	17.5
9	18.9	3.7	2.4	1.4	2.3	1.7	9.3
10	29.5	13.0	1.9	1.2	0.9	1.5	1.2
11	12.4	20.2	6.4	0.9	0.8	0.6	1.1
12	10.2	8.6	12.2	3.7	0.6	0.5	0.4
13+	19.9	16.5	25.1	30.9	16.3	19.0	2.9

M=0.20

Age	1980	1981	1982	1983	1984	1985	1986
5	12.9	8.7	33.7	42.3	23.1	44.3	24.5
6	7.9	10.3	6.5	25.2	32.6	18.5	35.4
7	5.5	6.0	6.4	4.0	18.4	23.7	13.8
8	6.0	4.1	3.5	3.5	2.6	12.3	16.0
9	21.1	4.1	2.6	1.5	2.3	1.6	8.4
10	33.0	14.1	2.0	1.3	0.9	1.5	1.1
11	13.6	22.0	6.9	1.0	0.8	0.6	1.0
12	10.6	9.1	12.9	3.9	0.6	0.5	0.4
13+	20.8	17.4	26.6	32.4	16.6	18.6	2.6

Table 6. Estimates of population size (millions of fish) of widow rockfish by age and year, obtained by catch-at-age analysis with lambda=0.5.

M=0.15

Age	1980	1981	1982	1983	1984	1985	1986
5	11.4	7.8	29.1	43.3	17.9	33.1	19.0
6	7.8	9.4	6.2	22.7	35.6	14.8	27.5
7	4.6	6.1	6.5	4.0	17.1	27.3	11.6
8	5.4	3.4	3.7	3.7	2.8	12.4	20.5
9	17.1	4.0	2.0	2.0	2.5	2.0	9.2
10	33.3	12.2	2.2	1.0	1.4	1.8	1.5
11	14.4	23.8	6.9	1.1	0.7	0.9	1.3
12	15.3	10.4	13.6	3.5	0.8	0.5	0.7
13+	34.3	38.8	34.5	31.6	27.0	21.7	17.7

M=0.20

Age	1980	1981	1982	1983	1984	1985	1986
5	13.2	8.8	32.2	46.1	18.1	31.9	17.3
6	8.9	10.5	6.7	24.0	36.1	14.3	25.2
7	5.2	6.7	7.0	4.2	17.3	26.3	10.6
8	6.1	3.8	4.0	3.9	2.9	11.9	18.6
9	19.2	4.3	2.2	2.1	2.6	1.9	8.3
10	37.7	13.3	2.4	1.1	1.4	1.7	1.3
11	16.5	26.1	7.4	1.2	0.7	0.9	1.1
12	17.4	11.5	14.7	3.7	0.8	0.5	0.6
13+	36.3	40.2	34.6	30.9	25.2	19.1	14.6

Table 7. Estimates from cohort (GENCOH) and catch-at-age (CAGEAN) analysis of widow rockfish biomass and spawning stock (thousands of metric tons) from 1980 through 1988. Estimates for 1987 and 1988 from the current assessment (87 GENCOH and 87 CAGEAN) are averages for three recruitment cases, using projected number-at-age vectors. Similar projections were made for 1986 and 1987 in the 1986 assessment (86 GENCOH).

Biomass

Year	M=0.15			M=0.20		
	86 GENCOH	87 GENCOH	87 CAGEAN	86 GENCOH	87 GENCOH	87 CAGEAN
1980	147.5	129.2	164.2	164.4	141.2	182.2
1981	99.6	96.4	138.5	108.0	104.1	148.3
1982	92.8	93.9	111.7	99.4	100.8	116.8
1984	76.1	76.7	93.9	77.5	77.9	91.8
1985	88.4	98.4	96.1	86.0	95.3	89.7
1986	87.4	80.3	94.2	83.7	73.0	83.1
1987	83.3	80.8	89.8	73.8	72.5	78.5
1988		74.0	79.6		65.9	68.2

Spawning stock

Year	M=0.15			M=0.20		
	86 GENCOH	87 GENCOH	87 CAGEAN	86 GENCOH	87 GENCOH	87 CAGEAN
1980	134.9	116.6	151.1	150.0	126.9	167.2
1981	88.5	85.3	127.1	95.7	91.8	135.6
1982	75.7	75.9	93.8	80.6	80.8	97.1
1983	67.6	67.4	69.5	71.3	71.1	69.6
1984	45.8	46.6	64.3	46.7	47.3	61.1
1985	60.6	61.4	66.4	59.0	59.8	61.1
1986	60.0	42.5	65.6	55.8	38.6	57.0
1987	59.7	51.3	66.2	48.1	44.0	54.7
1988		52.0	60.2		43.0	47.2

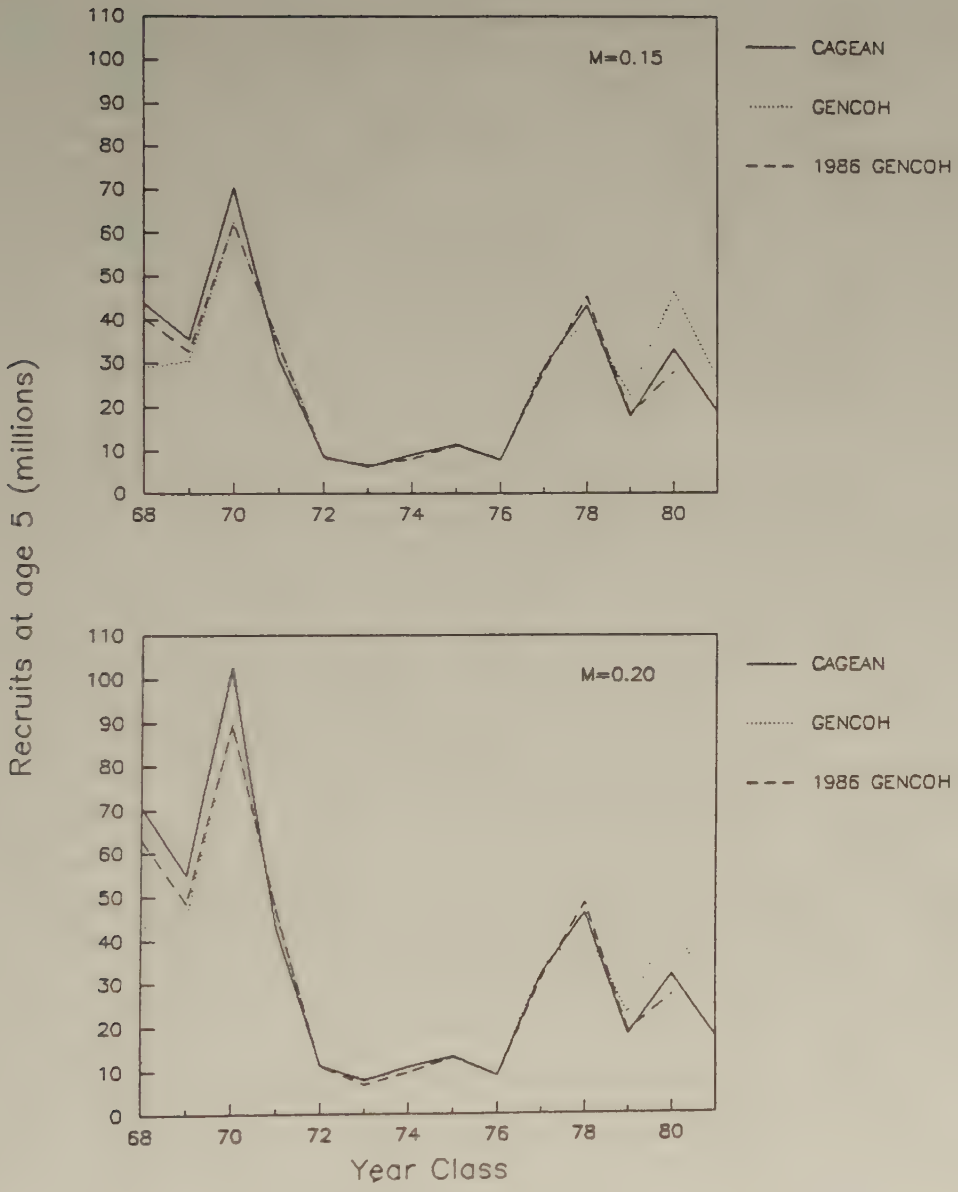

Figure 4. Estimates of widow rockfish recruitment at age 5 obtained from cohort (GENCOH) and catch-at-age analysis (CAGEAN). Estimates from the 1986 assessment (1986 GENCOH) are included for comparison.

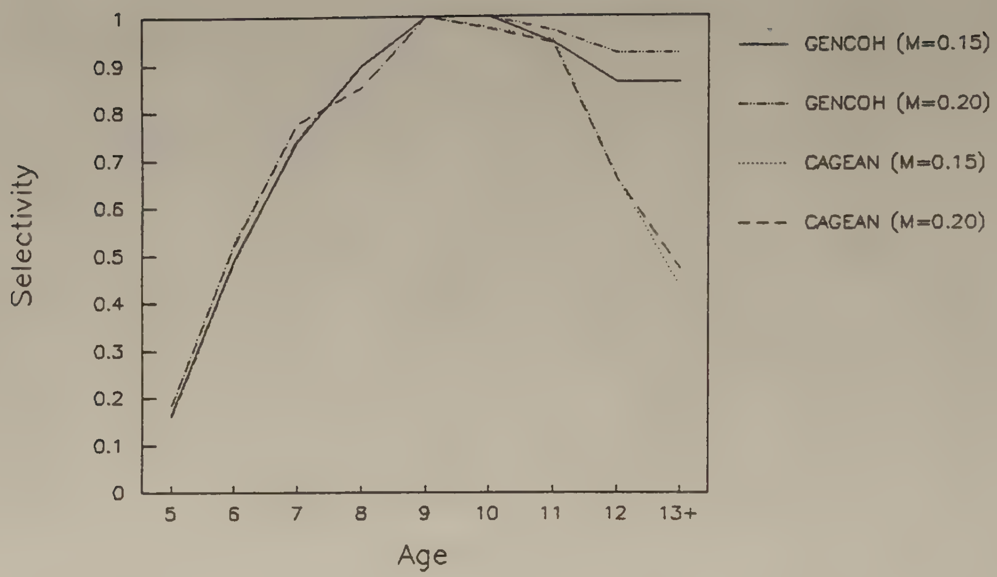

Figure 5. Estimates of age-specific selectivity for widow rockfish obtained by cohort (GENCOH) and catch-at-age analysis (CAGEAN) at two levels of natural mortality.

older fish in 1986 may be simply a random event or due to sampling error or errors in aging. Either possibility would cause cohort analysis to underestimate the number of age-13+ fish and stock biomass. An additional effect of the high $F_{12}(1986)$ in the cohort analysis is that estimates of $F_{12}(1980)$ are substantially higher than estimates in the 1986 assessment. This change results in a lower estimate of $N_{12}(1980)$, which is used to estimate the size of the 1968 year class (Figure 4).

One effect of the difference in selectivity patterns is that the estimated number of age-13+ fish differs substantially in some years for cohort and catch-at-age analysis (Tables 5 and 6). Results from catch-at-age analysis indicate that F_{13+} is less than F_{12}; therefore, estimates of N_{13+} and of stock biomass are generally higher than those from cohort analysis (Figure 6). Estimates of biomass at ages 5-12 are quite similar for the two approaches (Figure 6). Closer agreement in estimates of total biomass could be obtained by using some other assumption to estimate F_{13+} in cohort analysis.

Equilibrium yield curves from cohort and catch-at-age analysis were similar to each other and to curves obtained in the 1986 assessment. As in earlier years, it appears that an F of 0.30 for fully recruited fish (age 9) provides about the maximum yield if a stock-recruitment relationship exists and does not extract a large penalty if no relationship exists (Figures 7-8). Assuming that MSY would be obtained at that level of effort, estimates of MSY from cohort analysis results range from 7,700 to 12,000 mt, with an average of 10,100 mt. Using results of catch-at-age analysis, estimates of MSY ranged from 7,800 to 12,200 mt, with an average of 10,200 mt.

Equilibrium yield curves provide an indication of the average productivity of a stock; however, they fail to account for the short-term effects of variations in year class strength. We used a constant effort policy with $F_9=0.30$ to forecast yields from 1988 to 1992, starting from the estimated number-at-age vector for 1988 (Table 8). The average yield would be 12,400-13,100 mt in 1987 and 11,100-11,900 mt in 1988, with an average of 12,500 mt from cohort analysis and 11,700 from catch-at-age analysis. The estimate from cohort analysis is equal to the 1987 ABC and OY, while the estimate from catch-at-age analysis is about 10 percent lower. Both analyses predict that a moderate reduction in landings will be warranted in 1990-1992 when the presumably weak 1983 year class is fully recruited. It appears that the ABC estimate from cohort analysis remains unchanged from the 1986 assessment because the upward revision in the size of the 1980 year class (Figure 4) offset the downward revision in the abundance of age-13+ fish (Table 5).

Another approach for evaluating the short-term effects of variations in year class strength is to determine the sequence of fishing mortality rates needed to maintain a constant harvest. Using results from cohort analysis, we determined the levels of fishing mortality needed to produce constant yields of 9,000-15,000 mt (Table 9). Yields of 12,000-13,000 could be taken in 1988 and 1989, although a reduction in harvest would appear to be warranted by 1990.

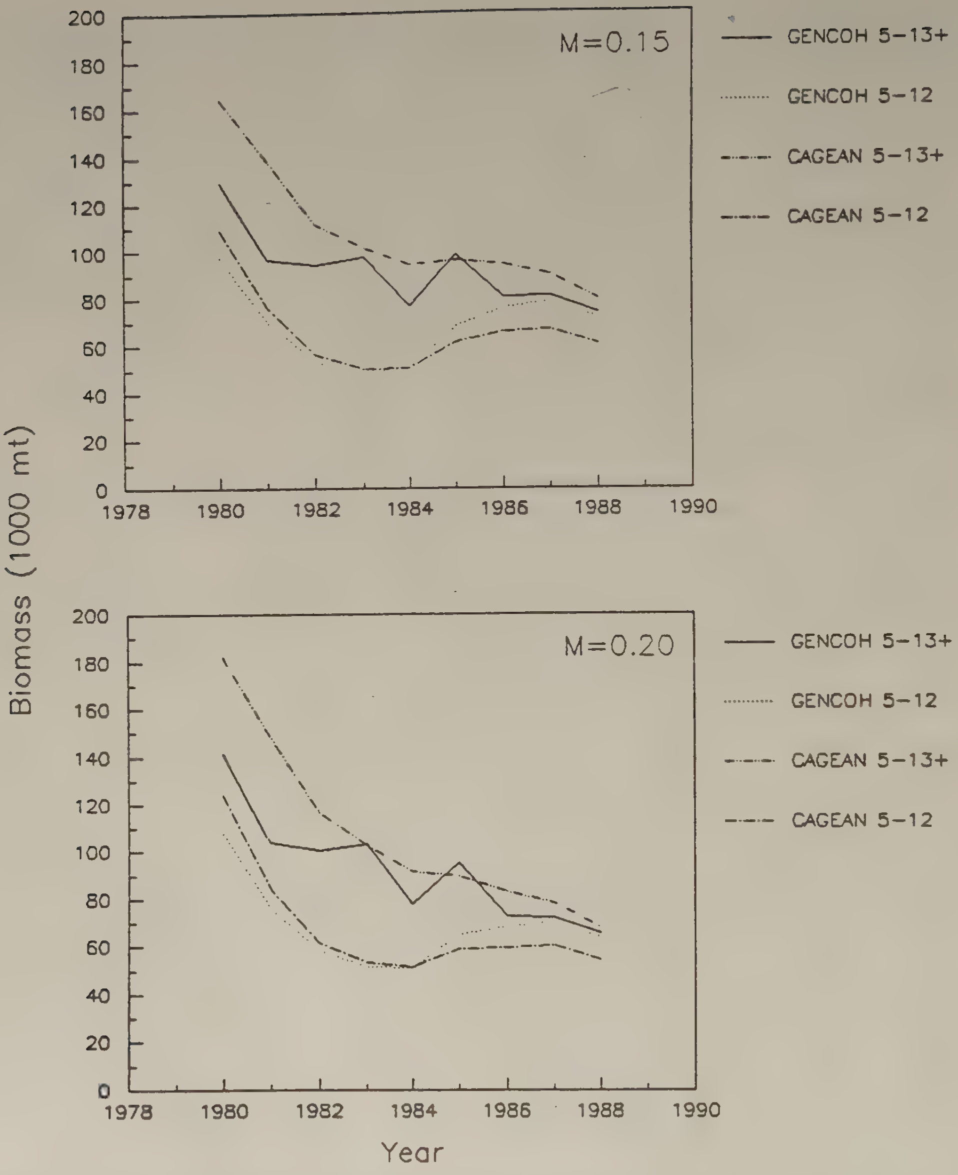

Figure 6. Estimates of widow rockfish biomass obtained by cohort (GENCOH) and catch-at-age analysis (CAGEAN) at two levels of natural mortality.

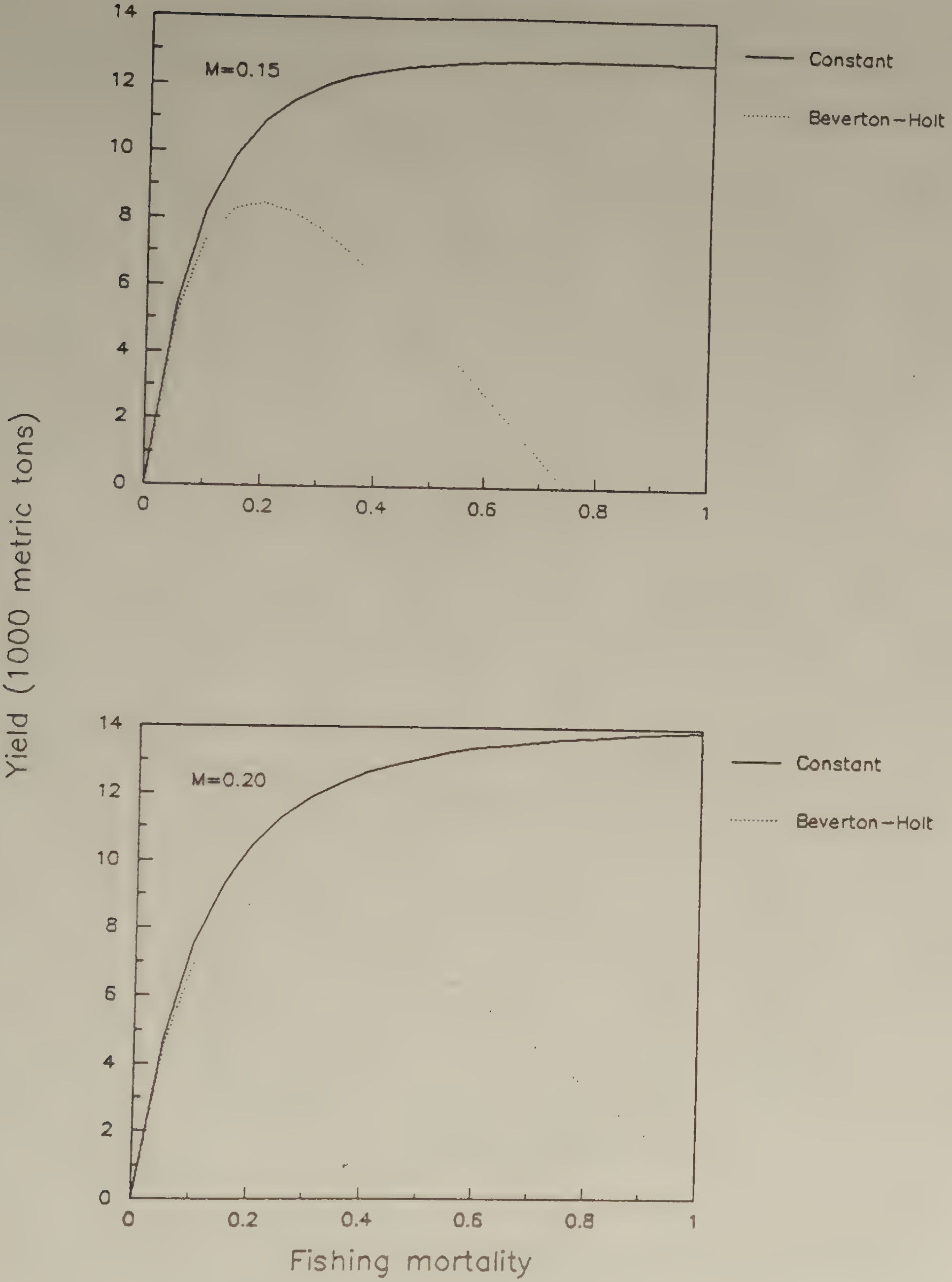

Figure 7. Estimates of equilibrium yield for widow rockfish based on results from cohort analysis.

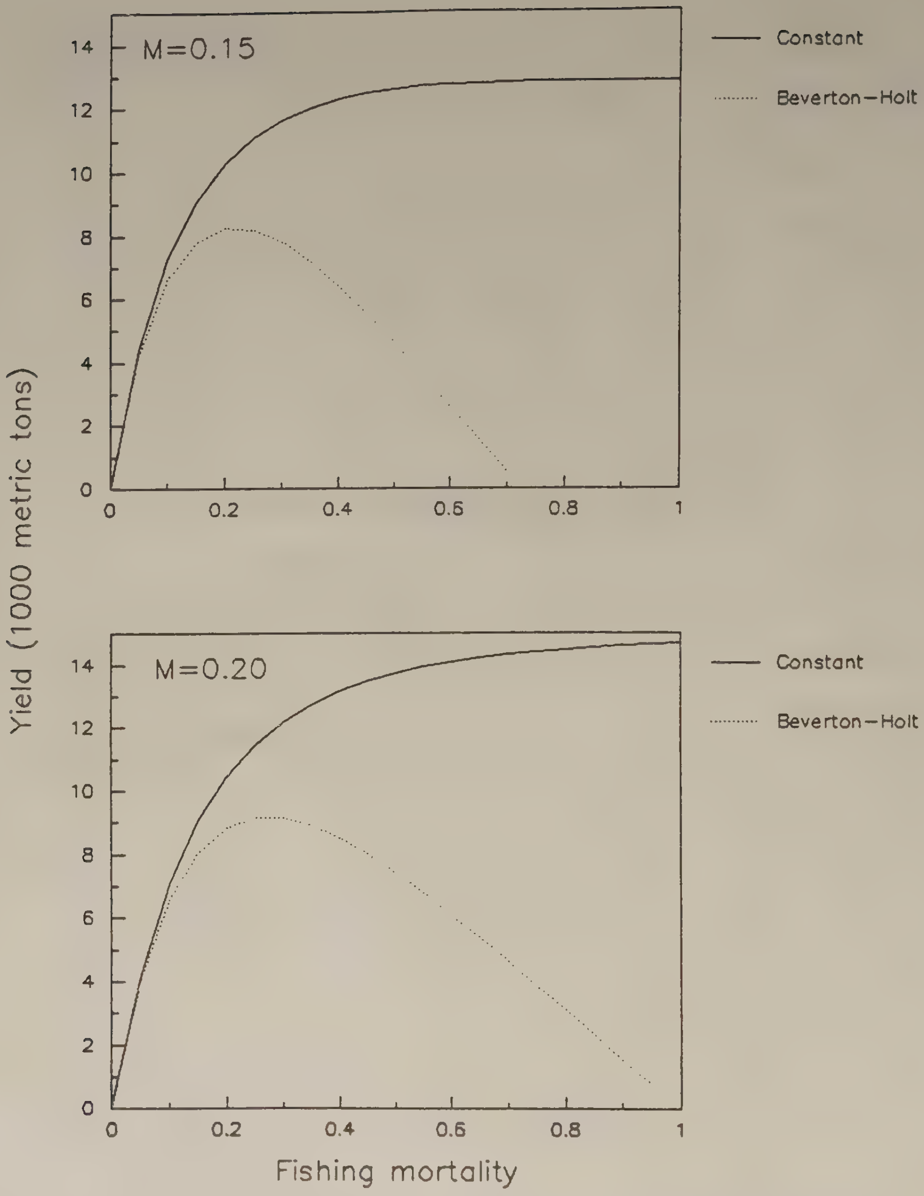

Figure 8. Estimates of equilibrium yield for widow rockfish based on results from catch-at-age analysis.

Table 8. Estimated yield (thousands of metric tons) when F for fully recruited fish is 0.3 for two values of M and three assumptions about recruitment.

Cohort analysis
Recruitment

	High		Low		Beverton-Holt		Average
Year	M=0.15	M=0.20	M=0.15	M=0.20	M=0.15	M=0.20	
1988	14.7	12.3	13.5	10.9	14.7	12.5	13.1
1989	13.5	11.3	11.6	9.3	13.7	11.9	11.9
1990	12.6	10.9	10.4	8.7	12.6	11.5	11.1
1991	12.1	10.9	10.1	8.9	11.8	11.1	10.8
1992	11.9	11.1	10.4	9.7	11.0	10.7	10.8
Average	13.0	11.3	11.2	9.5	12.8	11.5	11.5

Average for 1988 and 1989 (estimate of ABC): 12.5

Catch-at-age analysis
Recruitment

	High		Low		Beverton-Holt		Average
Year	M=0.15	M=0.20	M=0.15	M=0.20	M=0.15	M=0.20	
1988	14.1	11.6	12.7	9.7	14.2	12.0	12.4
1989	12.6	10.7	10.6	8.1	13.1	11.5	11.1
1990	11.6	10.3	9.5	7.9	11.9	11.1	10.4
1991	11.3	10.6	9.4	8.6	11.3	11.0	10.4
1992	11.2	11.0	9.8	9.5	10.9	10.9	10.6
Average	12.2	10.8	10.4	8.8	12.3	11.3	11.0

Average for 1988 and 1989 (estimate of ABC): 11.7

Table 9. Estimated F for fully recruited fish needed to maintain harvests of 9,000 to 15,000 metric tons for two values of M and three assumptions about recruitment.

		Recruitment						
Target harvest	Year	High		Low		Beverton-Holt		
		M=0.15	M=0.20	M=0.15	M=0.20	M=0.15	M=0.20	Average
9,000	1988	0.17	0.21	0.19	0.24	0.17	0.21	0.20
	1989	0.17	0.22	0.21	0.28	0.17	0.20	0.21
	1990	0.17	0.21	0.22	0.29	0.17	0.20	0.21
	1991	0.17	0.21	0.22	0.29	0.17	0.20	0.21
	1992	0.17	0.20	0.21	0.27	0.18	0.20	0.21
10,000	1988	0.20	0.24	0.21	0.27	0.20	0.23	0.23
	1989	0.20	0.25	0.24	0.32	0.19	0.23	0.24
	1990	0.20	0.25	0.25	0.35	0.20	0.24	0.25
	1991	0.20	0.25	0.26	0.35	0.20	0.24	0.25
	1992	0.20	0.24	0.26	0.33	0.21	0.24	0.25
11,000	1988	0.22	0.27	0.24	0.30	0.22	0.26	0.25
	1989	0.22	0.28	0.27	0.37	0.22	0.27	0.27
	1990	0.23	0.29	0.30	0.41	0.23	0.27	0.29
	1991	0.23	0.29	0.31	0.43	0.24	0.28	0.30
	1992	0.23	0.29	0.31	0.40	0.25	0.29	0.29
12,000	1988	0.24	0.29	0.26	0.33	0.24	0.29	0.28
	1989	0.25	0.32	0.30	0.42	0.25	0.30	0.31
	1990	0.26	0.34	0.34	0.49	0.26	0.31	0.33
	1991	0.27	0.35	0.37	0.52	0.28	0.33	0.35
	1992	0.28	0.35	0.38	0.50	0.30	0.35	0.36
13,000	1988	0.26	0.32	0.29	0.37	0.26	0.31	0.30
	1989	0.28	0.36	0.34	0.48	0.27	0.33	0.34
	1990	0.30	0.39	0.40	0.58	0.30	0.36	0.39
	1991	0.32	0.41	0.44	0.63	0.32	0.39	0.42
	1992	0.33	0.42	0.46	0.62	0.36	0.42	0.43
14,000	1988	0.28	0.35	0.31	0.40	0.28	0.34	0.33
	1989	0.31	0.40	0.38	0.54	0.30	0.37	0.38
	1990	0.34	0.44	0.46	0.68	0.33	0.41	0.44
	1991	0.37	0.48	0.52	0.77	0.37	0.45	0.49
	1992	0.39	0.50	0.56	0.79	0.43	0.51	0.53
15,000	1988	0.31	0.38	0.34	0.43	0.31	0.37	0.36
	1989	0.34	0.44	0.42	0.61	0.34	0.41	0.43
	1990	0.38	0.51	0.53	0.81	0.38	0.47	0.51
	1991	0.42	0.57	0.63	0.95	0.44	0.53	0.59
	1992	0.46	0.61	0.70	1.01	0.52	0.63	0.66

Discussion

Estimates of F-at-age and population size were generally similar for cohort analysis and catch-at-age analysis. A reasonable level of agreement would be expected since the same year-to-year changes in F were induced in both analyses. These additional assumptions were required in order to stabilize the estimates. Because the assumptions were based on our understanding of stock dynamics and of regulations controlling effort in the developing fishery, the resulting estimates should be more reliable than if no additional assumptions were made.

Estimates of long-term average productivity (average recruitment levels and MSY) from the 1986 and 1987 assessments were in close agreement. In addition, biomass estimates show an encouraging degree of stability from year to year, as have recent estimates of ABC. In the current assessment, both stock reconstruction techniques indicate that total biomass (ages 5+) has declined more or less steadily from 1980 to 1987. Biomass of fish ages 5-12 has been relatively stable after 1985, due to the strength of the 1977-1980 year classes. If, as expected, the 1983 year class is weak, a reduction in ABC to about 10,000 mt appears likely for 1989 or 1990. Better estimates will be possible once the size of the 1983 year class can be estimated from catch data.

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Autocatalytic pathways to cell death: a new analysis of the tuna burn problem

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Abstract

During capture and storage of tuna, a small but significant number of fish display a characteristic muscle degeneration termed tuna burn. Based on detailed amino acid analyses and on previous studies of metabolite changes during online swimming of tuna, a new model of the etiology of burnt muscle is developed. According to this model oxygen-lack to white muscle (developing initially during capture) leads to a metabolic collapse, to a drop in ATP concentration, to a consequent opening of ATP-dependent K^+ channels, with an efflux of K^+, and thus to a collapse of membrane potential. When the membrane potential falls far enough to open voltage-dependent Ca^{++} channels, Ca^{++} influx occurs leading to elevated Ca^{++} concentrations in the cytosol. This process is augmented by simultaneous movement of Ca^{++} from sarcoplasmic reticulum (SR) and from mitochondria into the cytosol. At high intracellular concentrations Ca^{++} can be devastating. One of its more notable effects involves the activation of Ca^{++}-dependent proteases, which preferentially target key components of the contractile machinery (troponins, tropomyosin, C-protein, M-protein, Z-discs, α-actinin) and thus cause disassembly of myofilaments prior to any significant hydrolysis of myosin or actin. This process is autocatalytic in the sense that Ca^{++}-activated proteases may act upon SR, thus increasing Na^+/Ca^{++} exchange, and ultimately adding more Ca^{++} to the cytosolic pool. According to this model, the difference between burnt and unburnt regions of the myotome is simply due to how far each region has moved along this self-destructive, autocatalytic pathway. The model is helpful in explaining previously perplexing data and in making useful (i.e. measurable) predictions for further studies of this important problem.

Introduction

Tuna burn is a term that has been coined for a state of muscle deterioration which is characterized by the development of a color that is paler than usual and a soft texture that implies some self-digestion. In Japanese literature, the analogous term is "yake", which literally means "spontaneously done meat" (Konagaya and Konagaya 1979). Although the time course of tissue deterioration is not precisely known, it appears to take at least several hours after capture to develop, and usually even longer. The extent of damage varies greatly, from as little as about 5% of the expaxial muscle mass to essentially 100% of it (Cramer *et al.* 1981). In addition, burnt tuna muscle is known to have high concentrations of lactate and the pH of extracellular fluid (ECF) is about pH 5.5–6 (Cramer *et al.* 1981). The latter is usually considered to reflect acidic intracellular fluid (ICF) which in turn is assumed to favor lysosomal acid proteases. In support of this assumption, direct measurements of soluble protein (as water extractable protein nitrogen) indicate that severely damaged samples sustain reductions down to about 50% of control values (Nakamura *et al.* 1977). The implicit model of tuna burn, then, favored by most earlier workers in this field can be summarized in the following metabolic scheme:

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metabolic acidosis → activation of acid proteases → self-digestion → muscle deterioration (burn)

To properly appreciate this proposed etiology of tuna burn, it is important to recall the metabolic conditions of the organism when captured online and brought on board a vessel. Because these teleosts are vigorous swimmers, perhaps unsurpassed in speed and manoeuverability, it is not surprising that after even a few minutes of online swimming, the metabolic state of skeletal muscles is greatly altered. The most drastic changes occur in white muscle, where tuna burn characteristically is found, and involve substrates, intermediates, and end products in energy metabolism. Glycogen and phosphocreatine (PCr) reserves are nearly fully depleted, with lactate and creatine being produced in stoichiometric amounts (Guppy *et al.* 1979; Hochachka 1980). In addition, ATP levels drop and this drop may be presumed to be stoichiometrically represented by an equivalent inosine monophosphate (IMP) accumulation. P_i is also assumed to accumulate in amounts equivalent to PCr depletion. These are standard effects observed in vertebrate white muscle in exhaustive work and their impact has been considered in detail elsewhere (Hochachka 1985a). From the perspective of this paper, the most important point to bear in mind is that the above metabolite concentration changes occur with a net acidification; i.e., H^+ also accumulates as a final metabolic end product which is widely assumed to be the most debilitating because it favors the above undesirable metabolic cascade. With this background, we reasoned that a simple test of the above theoretical burn etiology could be made by a detailed examination of the accumulation of amino acids as end products of acid-mediated proteolysis in damaged *vs* undamaged tuna white muscle.

Materials and methods

Samples of burned and unburned regions of the epaxial musle of yellowfin tuna were obtained from the commercial fishermen at Kewalo Basin, Honolulu. Weighed amounts of each sample were diced, then extracted in 0.6 M perchloric acid. The amino acid content and composition of each sample was then determined using a Beckman Amino Acid Analyzer as described elsewhere (Mommsen *et al.* 1980).

Results

The concentrations of all amino acids detectable in tuna muscle acid extracts are shown in Table 1. While the qualitative composition of the amino acid pool is not at all unusual for fish white muscle (Mommsen *et al.* 1980; Guppy 1978), the total pool size (averaging about 30–35 μmol g^{-1}) is some three fold higher than found in salmon under conditions of protein mobilization (Mommsen *et al.* 1980). However, by tuna standards, the pool size in these samples is actually smaller than in healthy unstressed individuals, mainly because of large depletions of histidine which obviously occur post-mortem. Histidine levels in these samples are in the 30 μmol g^{-1} range, compared to values some three fold higher in unstressed tuna (Abe *et al.* 1986).

Three additional points need emphasis: Firstly, whereas the generally elevated levels of amino acids are consistent with overall proteolysis occurring in tuna white muscle post mortem, no major differences are detectable between burnt and control sampling sites. The cause of burn, therefore, must be more subtle than the mere presence or absence of general proteolysis. Secondly, the pattern obtained is grossly different from that found in fish muscle which is actively mobilizing protein as a carbon and energy source (Table 2; also see Mommsen *et al.*

Table 1. Acid-extractable amino acid profile in burnt tuna white muscle compared to control (unburnt) samples taken from the same animals, expressed in nmoles g^{-1} wet weight of tissue

Amino acid	Concentration* Control	Burnt
taurine	560.7 (trace–988)	509 (23–855)
aspartate	trace	trace
threonine	636 (237–832)	608 (311–936)
serine	733 (594–804)	809 (572–1092)
asparagine	trace	trace
glutamate	1559 (1227–1979)	1534 (877–2409)
glutamine	334 (128–450)	400 (133–900)
proline	110 (trace–188)	225 (trace–458)
glycine	1666 (696–2470)	1726 (650–3005)
alanine	1718 (941–2217)	1719 (933–2572)
citrulline	trace	trace
valine	1094 (812–1364)	1152 (1006–1360)
methionine	212 (174–265)	187 (139–216)
isoleucine	508 (329–619)	492 (398–670)
leucine	837 (713–907)	838 (691–980)
tyrosine	261 (150–366)	263 (169–329)
phenylalanine	229 (119–335)	193 (104–303)
ornithine	359 (223–520)	409 (315–464)
lysine	2382 (1555–2863)	2198 (1663–2625)
histidine	19929 (16202–23508)	17889 (13587–22812)
3-methyl-histidine	trace	trace–92
arginine	226 (163–271)	336 (244–466)
anserine	52080 (44979–55995)	51313 (48395–52992)

*Average of three samples, with range of values given in brackets below. Muscle samples were graded as slightly, moderately, or heavily burnt, but since in any given animal these did not differ from control values in the same animal, all data are pooled. In individuals showing heavily burnt regions, dominant, metabolically active amino acids (each as glutamate, glycine, and alanine) occurred at 2–3 higher fold concentrations in control and burnt samples than they did in similar samples from individuals showing less severe burn damage. Thus we conclude that this difference simply represents differing amounts of generalized proteolysis (perhaps due to longer post-mortem periods prior to sampling) and does not relate directly to the etiology of burn.

Table 2. Several metabolically active amino acids in burnt and control tuna muscle (expressed as mole fraction of total amino acid pool and compared to fish muscle that is actively mobilizing protein)

Amino acid	Unburnt control	Burnt muscle	*In vivo* fish muscle metabolizing protein*
aspartate	0.2	0.2	1–4
glutamate	4.7 (3.6–5.4)	4.7 (2.5–6.7)	7
glycine	5.0 (2.0–6.7)	5.3 (1.9–8.3)	10
alanine	5.2 (2.7–6.9)	5.4 (2.7–7.2)	20–30
lysine	7.0 (5.3–8.3)	6.8 (6.3–7.7)	3–7
histidine	59.7 (54.9–68.1)	55.6 (48.1–66.8)	3–36
arginine	0.7 (0.5–0.8	1.0 (0.8–1.3)	2–3

*From Mommsen *et al.* (1980). The similarity between unburned control and burned samples again supports the conclusion that generalized proteolysis is similar in both regions; the difference between them seems to reside mainly in the disassembly of myofilaments in burned mytomal regions. The marked difference between post-mortem muscle and fish muscle actively metabolizing protein as a fuel is assumed to reflect a loss of metabolic regulation of proteolysis in post-mortem muscle.

1980), which might be anticipated if the post-mortem proteolysis was not under metabolic control; in fish actively utilizing protein as a fuel, proteolysis is clearly closely regulated (Hochachka and Somero 1984). Thirdly, the absence of significant levels of 3-methyl-histidine is a most significant result of these analyses (Tables 1 and 3). This animo acid occurs only in the white muscle isoforms of myosin and in actin and is so accurate a marker (Tonomura 1973) that its release rate is utilizable as a means for quantifying the rate of breakdown of these proteins (Lowell *et al.* 1986). In our samples, 3-methyl-histidine is found at modest levels only in burned muscle (Tables 1 and 3); its occurrence at low levels in most of our extracts means that myosin and actin are **not** hydrolyzed to any appreciable degree under capture and initial boat-storage conditions.

Table 3. Observed and theoretical maximum levels of 3-methyl-histidine in burnt tuna muscle

Burn condition	3-methyl-histidine	Approx. theoretical maximum*
slight	trace	500
moderate	trace	500
heavy	92	500

*Assuming complete hydrolysis of myofilaments. The white muscle isoform of myosin is assumed to occur at 0.1 μmol per g muscle and contain two moles of 3-methyl-histidine per mol myosin; actin occurs at about 0.3 μmol per g muscle and contains one mol of 3-methyl-histidine per mol actin (Tonomura 1973).

Discussion

The protease paradox

In considering the above information, two conclusions can be made with confidence. On the one hand, breakdown of tissue texture (in the extreme, to a seemingly self-digested muscle) implies a breakdown of myofibers in tuna burn. On the other hand, the absence of 3-methyl-histidine in appreciable quantities emphatically rules out extensive hydrolysis of myosin and actin, the two dominant proteins of muscle fibers. In trying to resolve this paradox, it is necessary to retrace our steps to reconsider what is currently known of mechanisms in cell death and in subsequent proteolysis. In the process, new insights are gained on the etiology of tuna burn.

Decoupling metabolic and membrane functions

From recent analyses of this problem (Hochachka 1986) it is evident that O_2-lack and a consequent drop in ATP synthesis rates initiates an autocatalytic cascade leading to cell damage and cell death (Fig. 1). Most animal tissues under these conditions are unable to maintain a balance between the rates of ATP hydrolysis required by ion pumps and rates of ATP synthesis achievable by energy metabolism. Metabolic and membrane functions consequently become decoupled, a process manifest in a large K^+ efflux, followed by a Na^+ influx, as ICF and ECF pools move towards equilibrium positions. Dropping ATP level, by favoring opening of K^+ channels (Spruce *et al.* 1985), may be the metabolic signal which initiates this membrane-metabolism decoupling. Be that as it may, when the membrane potential drops sufficiently, voltage-dependent Ca^{++} channels are opened which lead to a large influx of ECF Ca^{++}, a process favored by a very large ECF – ICF concentration gradient, and leading to increasing $[Ca^{++}]$ in the cytosol. Increased Ca^{++} levels in the cytosol are also favored by increased Na^+/Ca^{++} exchange at the cell membrane, and possibly at the mitochondria, as well as by Ca^{++} leakage from the sarcoplasmic reticulum (SR).

Although Ca^{++} at low concentrations plays many pivotal functions in cell regulation and signal transduction, at high concentrations it is a known intracellular toxin, (see Hochachka 1985b for literature). Under conditions of tuna capture and boat-storage, we propose that one of its most debilitating actions occurs via the activation of Ca^{++}-dependent proteases in muscle. The literature on Ca^{++}-activated proteases is vast and we cannot review it all here (see Zeman *et al.* 1985). Suffice to emphasize that for some half-decade now it has been known that these proteases preferentially and selectively degrade specific components of the contractile machinery: troponin, tropomyosin, C-protein, and M-protein (Bird *et al.* 1980). Later studies show Ca^{++}-induced weakening of Z-discs (Hattori and Takahashi 1982) and a stringent requirement for Ca^{++} in the subsequent complete removal of Z-lines and α-actinin by Ca^{++}-activated neutral proteases (Reddy *et al.* 1983). If uncontrolled, as may be expected in tuna burn, these effects of course are severely damaging and they are exacerbated by proteinases acting on the SR so as to increase Na^+/Ca^{++} exchange and thus further add to the ICF Ca^{++} pool (Phillipson and Nishimoto 1982).

The net effect of Ca^{++}-activated protease function is the disassembly of myofilaments prior to any significant degradation of myosin or actin (Bird et al. 1980). As this is exactly what seems to be observed in tuna burn, we propose that the above protease paradox can be fully resolved on the as-

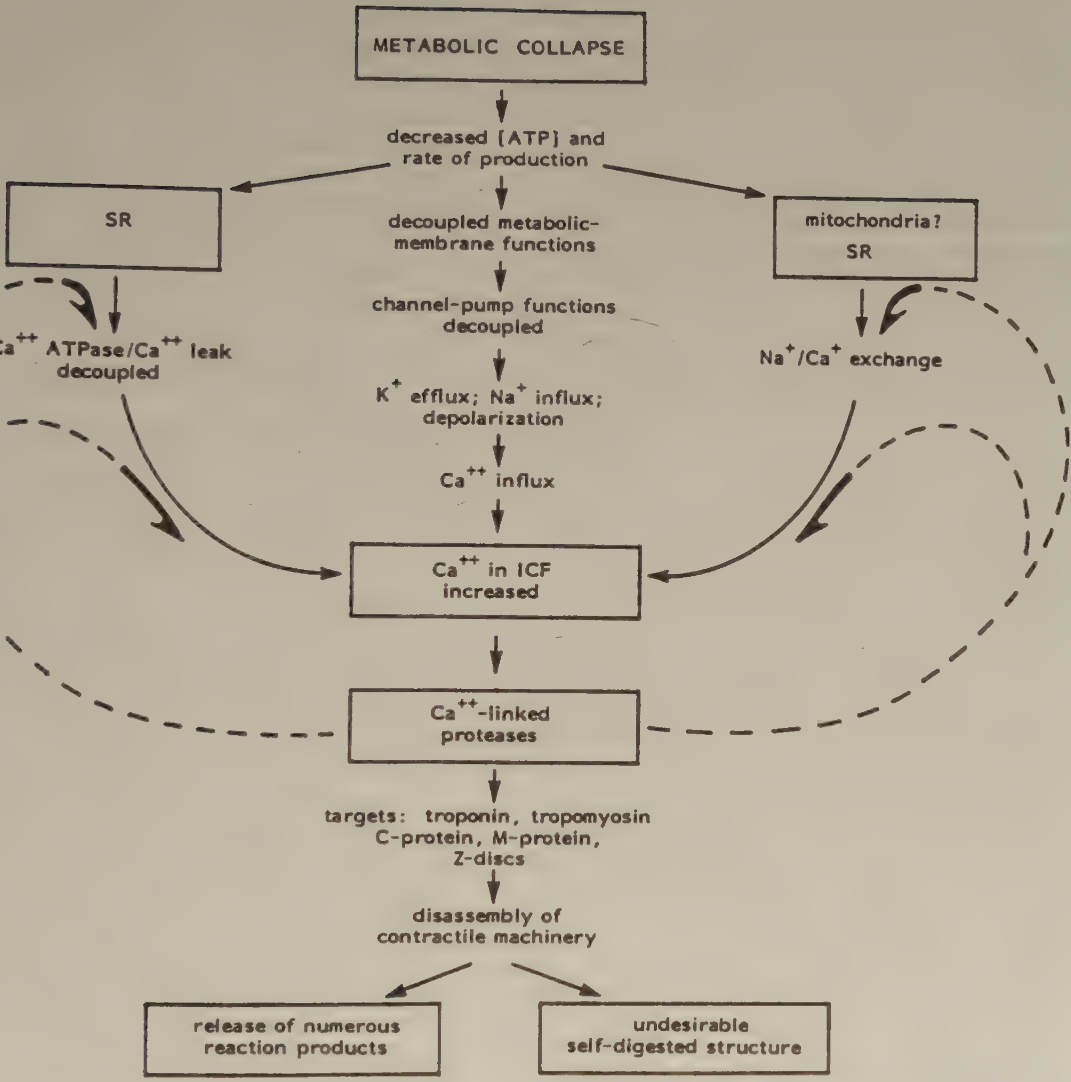
METABOLIC COLLAPSE
decreased [ATP] and rate of production
SR
decoupled metabolic-membrane functions
mitochondria?
SR
Ca^{++} ATPase/Ca^{++} leak decoupled
channel-pump functions decoupled
Na^{+}/Ca^{+} exchange
K^{+} efflux; Na^{+} influx; depolarization
Ca^{++} influx
Ca^{++} in ICF increased
Ca^{++}-linked proteases
targets: troponin, tropomyosin C-protein, M-protein, Z-discs
disassembly of contractile machinery
release of numerous reaction products
undesirable self-digested structure

Fig. 1. Proposed model of metabolic events initiated during online capture of tuna and terminating in burnt muscle in post-mortem tuna.

sumption that Ca^{++}-dependent protease function is the initial tissue-damaging step in the development of burn.

The metabolic scenario emerging from this analysis, therefore, is the following (see Fig. 1):

metabolic collapse (due initially to O_2 lack) → membrane collapse (K^{+} efflux) → rise in Ca^{++} ICF concentration (from ECF, SR, and mitochondrial pools) → proteolysis of minor structural components; disassembly of myofilaments → undesirable texture development prior to actual hydrolysis of myosin and actin

Models such as this one are useful if they allow explanations of previously perplexing data and if they lead to testable predictions. With respect to the former criterion, our model satisfactorily explains the main paradoxical finding of this study: development of a soft, self-digested muscle texture in the absence of myosin and actin hydrolysis (in the absence of significant amounts of 3-methyl-histidine accumulation (Table 3)). Additionally, the model better explains why self-digested texture can appear in the absence of severe acidosis: Ca^{++}-dependent proteases typically display near-neutral pH requirements while the classical lysosomal proteases considered the most likely candidates for proteolysis in earlier burn studies require very acidic conditions (about pH 4.5) for activity (see Bird *et al.* 1980; Zeman *et al.* 1985, for further literature).

In this context, it may be useful to mention that previous workers interested in tuna muscle deterioration have placed especial focus on end product accumulation, in particular lactate and H^+ accumulation. The reason for such emphasis, of course, was the implicit assumption that low pH is required for extensive tissue proteolysis. However, we now feel that such emphasis may be premature and perhaps unjustified. Whereas glycogen and lactate are utilized and accumulated in stoichiometric amounts, accumulation of H^+ is not stoichiometric with the accumulation of lactate because much of the protons produced are effectively absorbed by intracellular buffers. Aside from proteins, tuna white muscle typically has two additional sources of very effective intracellular buffers: phosphate which accumulates under these conditions, and histidine plus histidine related compounds (anserine and carnosine), which in total are found in tuna white muscle at over 100 μmol g^{-1} (Abe *et al.* 1985, 1986). Even in post-mortem muscle samples these total about 70 μmol per g tissue (Table 1). Thus, while extracellular pH may drop to pH 5.5–pH 6 within a few hours of capture of the animal (Cramer *et al.* 1981), intracellular H^+ concentrations may or may not mimic this pattern, and thus pH_i values may not fall this low. Nevertheless, no one would argue that the pH_i probably is well below pH 7; a value of pH 6–6.5 is not unreasonable based on known end products and buffering components (Abe *et al.* 1985). This value is consistent with Ca^{++}-protease function, but inconsistent with extensive lysosomal tissue degradation. Thus our model can readily explain a previously perplexing situation – proteolysis without drastic acidification.

In addition to helping us understand features of tuna burn that are already known, our model makes several specific, and highly testable predictions. Perhaps the most useful (i.e. easily measurable) of such predictions are the following:

(i) K^+_{ECF} concentrations in burnt tuna muscle should exceed values in control nonburnt samples.
(ii) Ca^{++}_{ICF} concentrations in burnt tuna muscle should exceed values in control nonburnt samples.
(iii) Troponin/tropomyosin breakdown intermediates should occur in higher concentration in burned muscle than in unburned samples.
(iv) Troponin or tropomyosin concentrations in burnt tuna muscle should be less than in nonburnt control samples; in severely burnt muscle, even myosin and actin hydrolysis should occur (Pemrick and Grebenau 1984).
(v) In the event of (iv) above, the concentration of 3-methyl-histidine (from actin and myosin) in severely burnt tuna muscle should exceed that in nonburnt control samples. (This result is implied in Table 3 but needs reconfirmation with larger sample numbers).

Finally, in our view, since the degenerative cascade process probably begins during online capture, the main difference between burnt tuna muscle and nonburnt post-mortem muscle is in how far along the autocatalytic, self-destructive pathway (of Fig. 1) each tissue region has progressed. The difference between burnt and normal post-mortem tuna muscle may be quantitative and perhaps less drastic than previously supposed.

Acknowledgements

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ESTIMATING DENSITY OF DOLPHIN SCHOOLS IN THE EASTERN TROPICAL PACIFIC OCEAN BY LINE TRANSECT METHODS

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ABSTRACT

Data were collected from aerial and research ship surveys to estimate density of dolphin schools in the eastern tropical Pacific using line transect (LT) theory. The surveys were conducted from 1977 through 1983. Several assumptions of LT theory were investigated for both aerial and ship data. Factors were developed to alleviate effects of suspected violations of the assumptions. I estimated densities from data stratified into an inshore area surveyed by planes and an offshore area surveyed by ships. The density estimate for the inshore area was 4.18 schools/1,000 km^2 and 2.04 for the offshore area. For the entire area, the density estimate was 2.71 schools/1,000 km^2. Adjustments for possible biases owing to adverse sea state and sun glare conditions increased the inshore estimate by 8% and the total area estimate by 4%.

The National Marine Fisheries Service (NMFS) is responsible for assessing the status of those dolphin stocks taken incidentally by tuna purse seiners in the eastern tropical Pacific (ETP) Ocean. Techniques used to assess these stocks (Smith 1979[2]) require estimates of school density, so density estimates were made in 1975 (Smith 1975[3]) and in 1979 (Holt and Powers 1982). Since 1979, NMFS has collected additional information to test the assumptions of its statistical methods and to further survey the areas inhabited by the dolphins. In this paper, I present analyses of data collected from 1977 through 1983 to determine density estimates of dolphin schools in the ETP. In addition, I investigate several factors which may bias the estimates.

To obtain estimates of density of dolphins (individuals) it is further necessary to consider school size, the proportions of various species in mixed schools, and areas inhabited by the various stocks. Estimation of these factors is complex; they are to be dealt with elsewhere and are not addressed in this paper.

MATERIAL AND METHODS

Surveys

Data used to calculate the density of dolphin schools were collected during several years. Aerial surveys were conducted in 1977 and 1979 (Fig. 1), and nine research ship cruises were made during 1977, 1979, 1980, 1982, and 1983 (Fig. 1). Most surveys were conducted between January and early April; one of the 1977 ship cruises was made in October and the two 1980 cruises were made from May through August.

A two-engine PBY amphibious patrol bomber was used in the 1977 aerial survey (SWFC 1978[4]), and a four-engine PBY bomber was used in the 1979 aerial survey (Jackson 1980[5]). Operating and viewing conditions aboard the two aircrafts were similar. Both planes cruised at 148-240 km/hour (80-130 kn) and had bubble-shaped waist windows. The PBY used in 1977 had a flat bow window which was shaped like an isosceles trapezoid. The 1979 PBY had a round bubble-shaped bow window. The round bubble window allowed

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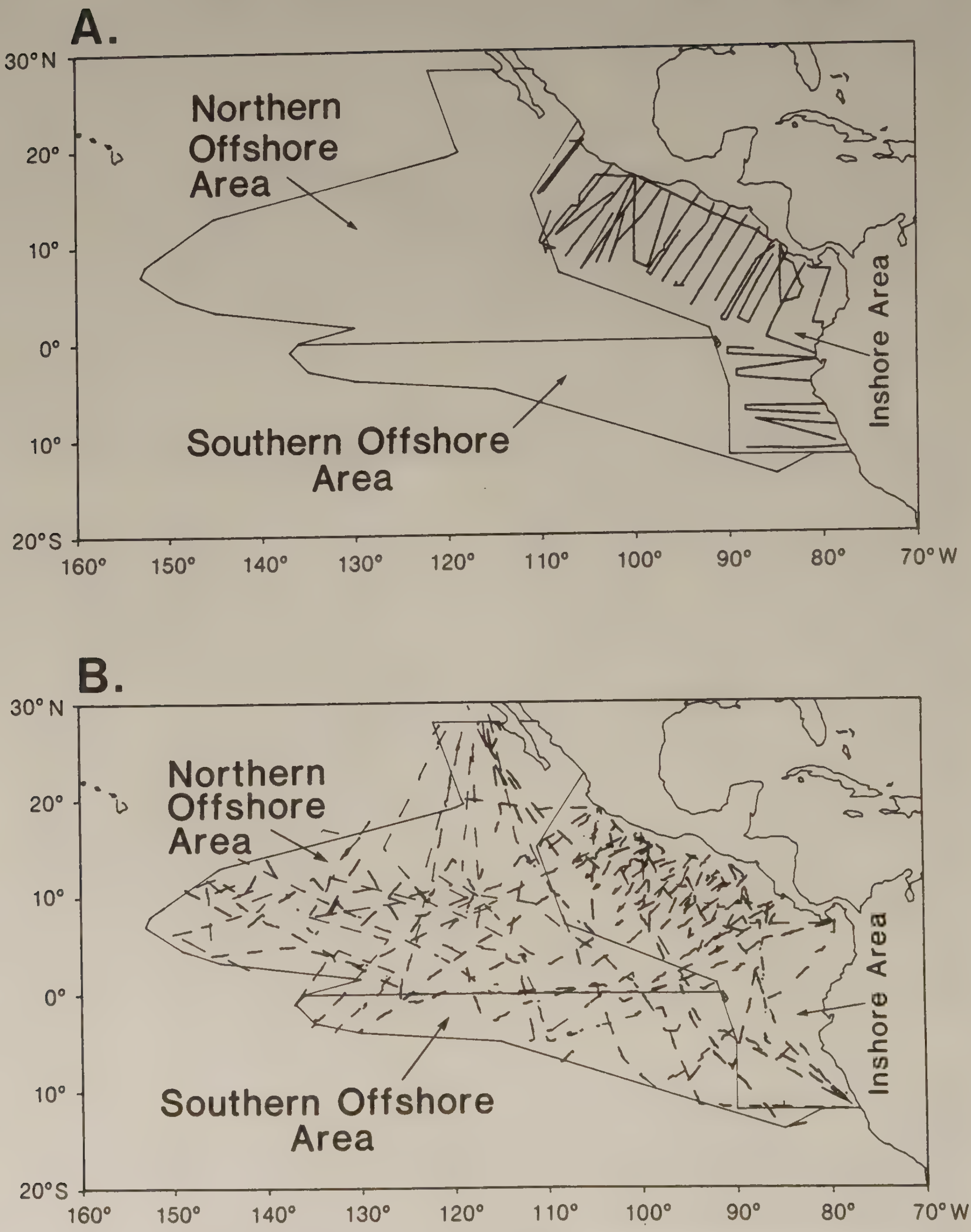
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Northern Offshore Area
Southern Offshore Area
Inshore Area

FIGURE 1.—Tracklines for 1977 and 1979 aerial (A) and combined 1977, 1979, 1980, 1982, and 1983 ship (B) surveys.

better lateral viewing, but both provided unobstructed forward and downward views.

Two research vessels were used to collect the shipboard data. The NOAA ship *David Starr Jordan* was used during all years and the NOAA ship *Townsend Cromwell* joined it in 1977, 1979, and 1980. Both vessels were similar in length and cruising ability. Binoculars used to locate animals were mounted approximately 10.7 m above the sea on the *Jordan* but were only 6.1 m above the sea on the *Cromwell*. In addition, observers aboard the *Jordan* used 20× binoculars during the 1977 surveys and 25× glasses on the rest of the surveys; observers aboard the *Cromwell* used only 20× glasses during their surveys. Consequently, viewing conditions were generally much better on the *Jordan*.

Study Area

Survey efforts traversed the combined range of ETP dolphin stocks defined by Au et al. (1979)[6]. The range was partitioned into "inshore" and "offshore" areas (Fig. 1). Airplanes were used to survey the inshore area, and ship surveys were conducted in both areas during each year, except during 1977 when ships surveyed only the offshore area.

Data Collection

Aerial Data

Data collecting procedures used during the aerial surveys are described by SWFC (fn. 4), Jackson (fn. 5), Holt and Powers (1982), and Cologne and Holt (1984)[7]. As the airplanes traversed predetermined tracklines (Fig. 1), the observers recorded schools on and to either side of the lines. Observers searched through the bow window and from windows located on either side of the plane. The bow observer was responsible for detecting schools on the trackline (a path underneath the plane 0.19 km wide). The searching mode was halted if environmental or oceanographic conditions restricted the observer's view of the trackline or when the plane was diverted from the trackline for closer examination of a school. Additional schools detected during these diversions were not included in the density analysis.

Sea conditions were measured on the Beaufort scale (Bowditch 1966), which ranged from very flat, glassy seas (Beaufort 0 conditions) to rough seas with numerous large, white-capped waves (Beaufort 5 conditions). Sun location was described by horizontal and vertical position relative to the bow observer (Holt 1983a). These were recorded for each segment of effort.

Biological and environmental data were recorded at each sighting (Holt and Powers 1982). Data included species identification, school size estimates, sea state, sun position, and perpendicular distance to the school from the trackline. School size estimates consisted of an observer's "best" estimate plus an estimate of the minimum and maximum range.

Ship Data

Shipboard collection procedures are described in the various cruise reports (unpublished documents available from the SWFC) and by Holt (1983b). Procedures and data recorded on shipboard surveys were similar to those for aerial surveys. Two observers used binoculars located on each side of the ship to search from directly ahead to abeam of their respective sides of the ship. Starting in 1979, sea state was recorded at the beginning of each effort segment (leg). Sun position was recorded during the 1982 and 1983 ship surveys.

The bearing (θ) and radial distance (r) to a school from the ship were recorded, and perpendicular distance (y) was then calculated as $y = r \sin \theta$. In surveys conducted before 1980, observers rounded estimates of sighting angles to multiples of 5° or 10°, and radial distances to multiples of 185 m (0.1 nmi) within the first 1.85 km (1 nmi), and to 0.93 km (0.5 nmi) multiples at larger distances (Fig. 2). During training, observers on the 1980 surveys were told of previous rounding inaccuracies and instructed to make estimates as precise as possible. However, they were still unable to make precise visual estimates of angles and distances for schools recorded at great distances from the ship (Fig. 2). During the 1982 and 1983 surveys, estimates of bearing were recorded using a 360° graduated washer attached to the base of the binoculars, and the radial distances were measured using a graduated reticle enclosed in the right eyepiece of the binoculars (Holt 1983b).

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[6] Au, D., W. Perryman, and W. Perrin. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. Southwest Fisheries Center Status of Porpoise Stocks working paper SOPS/79/36, 59 p.

[7] Cologne, J., and R. Holt. 1984. Observer effects in shipboard sight surveys of dolphin abundance. Southwest Fish. Cent. Adm. Rep. No. LJ-84-30, 42 p. National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

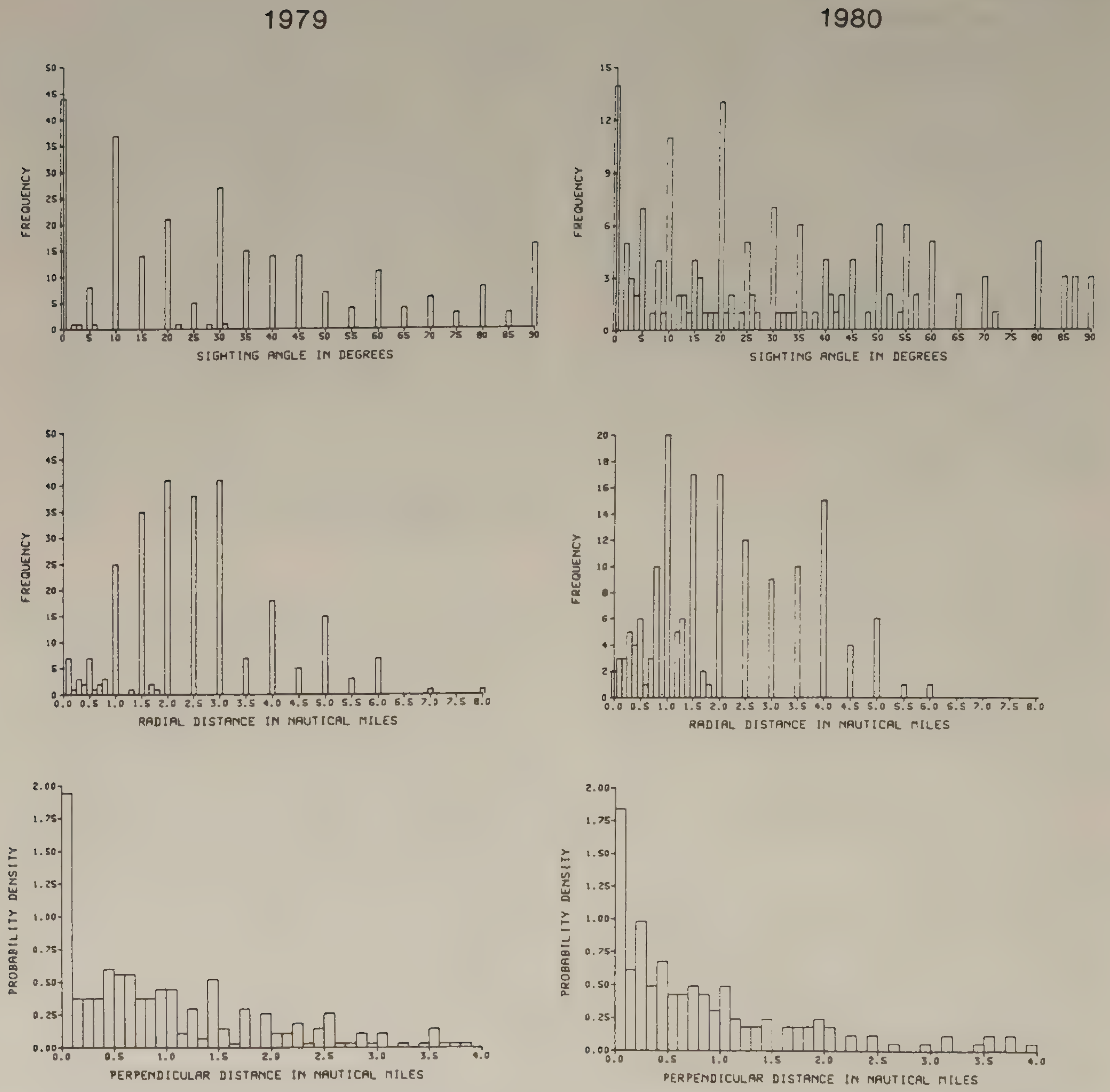

FIGURE 2.—Distribution of sighting angle, radial distance, and perpendicular distance from 1979, 1980,

With this system, the rounding to convenient values was not as evident (Fig. 2); however, measurements may still be inaccurate.

ANALYTICAL METHODS

Vessel data for area, sea state, sun glare, and observer performance strata were compared using rates of detection for all schools encountered within 2.13 km perpendicular distance of the ship (schools/1,000 km searched) and estimates of density of schools (schools/1,000 km^2). Similar comparisons of aerial data were completed using rates of detection for all schools encountered within 1.85 km perpendicular distance of the trackline, rates of detection for trackline schools, and estimates of school density.

Density estimates were made using line transect (LT) theory (Burnham et al. 1980). The basic equation (Seber 1973) is

$$D = \frac{n\, f(0)}{2L}$$

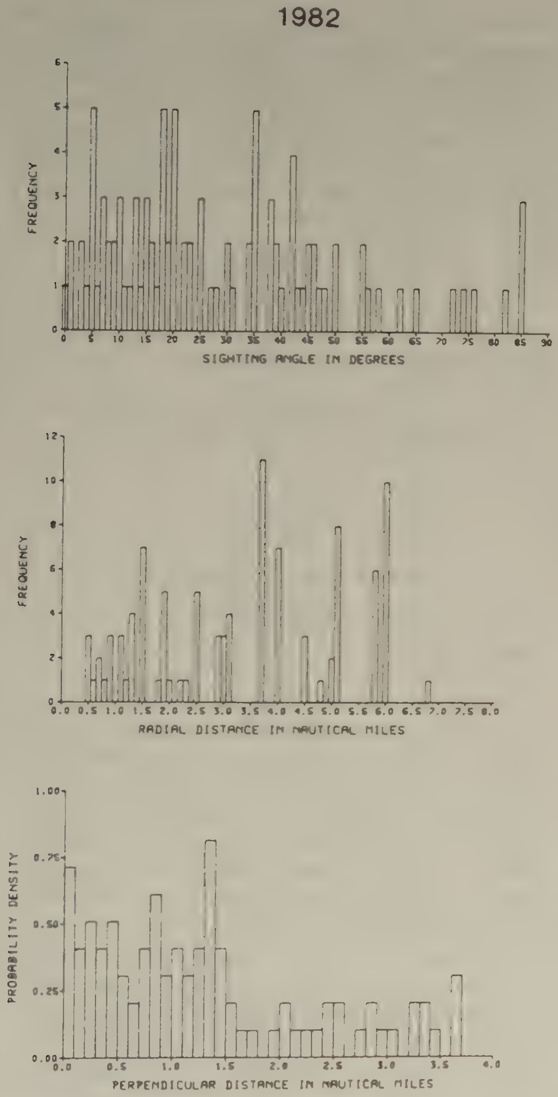

FIGURE 2.—*Continued*—and 1982 ship data.

where n is the number of schools sighted, D is the density of dolphin schools per km^2, L is the total linear distance searched (km), and $f(0)$ is a probability density function (*pdf*) evaluated at perpendicular distance, $x = 0$. The Fourier series (FS) model (Crain et al. 1979) was used to estimate $f(0)$ based upon criteria developed by Burnham et al. (1979). Burnham et al. (1980) is recommended for a full presentation of the FS model and for variance estimation.

Several assumptions must be met for valid use of LT theory. I investigated three of them for this study: 1) schools directly on the trackline are never missed, 2) schools do not move in response to the approaching ship or plane; and 3) no systematic measurement errors occur. All three assumptions have been made in analyzing previous aerial survey data (Holt and Powers 1982); however, field studies have subsequently been conducted to investigate the ability of observers to detect trackline schools (Holt 1983a), and whether or not dolphins avoid approaching ships (Au and Perryman 1982; Hewitt 1985). In addition, assumption 3 was not accepted because an inordinately large number of schools detected from the ships was recorded on the trackline.

Data Treatment

All species of dolphins encountered in the study area were included in the analyses. Of these, only schools with a mean minimum or mean best estimate of more than 14 animals were used because my field experience indicated that the probability that all animals in a school of at least this size would be submerged at one time, and hence undetectable, was very small. In addition, species affected by the fishery generally occur in schools with more than 14 animals.

During the first 18 of 20 flights of the 1979 aerial survey, two independent teams of three observers each searched for dolphin schools. Members of each team always searched for dolphins during the same time, alternating with the other team.

For aerial and 1979-83 ship data, observers recorded sea state conditions according to individual Beaufort, but during analyses, I grouped the data into 1) a "calm" sea state category: seas without whitecaps (Beaufort conditions 0-2) or 2) a "rough" sea category: seas with whitecaps (Beaufort conditions 3-5). Data for Beaufort conditions >5 were omitted from the analyses. The presence of whitecaps was important because animal splashes were used as sighting cues during calm conditions but could not be easily distinguished from whitecaps during rough conditions.

For aerial data and 1982-83 ship data, sun glare effects were investigated by classifying effort at various sun positions into "good" and "poor" categories depending on the amount of sun glare on the trackline (see Holt[8] for method used to record position of sun relative to the platform and for criteria used to define sun categories for aerial data). Criteria used for ship data were based upon observations recorded during a subsequent ship survey (Hohn[9]). Hohn found poor sun conditions on the trackline only when horizontal sun position was 12 and vertical position was 1, 2, or 3 or when clouds were accompanied by fog or rain. All other effort was defined as occurring during good conditions.

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[8] Holt, R. 1984. Testing the validity of line transect theory to estimate density of dolphin schools. Southwest Fish. Cent. Adm. Rep. No. LJ-84-31, 56 p. National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

In order to apply the Fourier series (FS) model to aerial and ship data, I structured the data by 1) selecting appropriate interval widths for grouping the perpendicular sighting distributions (data cutpoints), 2) choosing a maximum observation distance perpendicular to the trackline (truncation point), 3) developing criteria to select the appropriate number of terms for the FS model, and 4) choosing the type of transformation to use in compensating for measurement error in the shipboard data.

Based on a subset of the ship data (Holt[10]), I used an interval width of 0.37 km (0.2 nmi) and truncated the perpendicular distance distributions at 3.7 km (2.0 nmi). Since perpendicular distance distributions for the ship data, and also to a lesser extent for aerial data, have very prominent modes or "spikes" at the origin, existing criteria to select the appropriate number of terms in the FS model were unsatisfactory. Therefore, I selected the model which provided the best visual fit to the distributions near the origin (Holt fn. 10). This technique was easily applied and was consistent among data sets. For use of the technique I assumed that the sizes of the spikes near the origins of the perpendicular distance distributions were indicative of relative density among the data sets. To minimize the effects of recording errors, the data were smoothed using the technique "smearing" (Butterworth 1982; Hammond 1984).

Based on previous investigations of aerial data (Holt and Powers 1982), I selected a truncation point of 1.94 km (1.05 nmi) and an interval width of 0.19 km (0.1 nmi) for the aerial data. I used the same technique as used for ship data to select the appropriate number of terms in the FS models; however, the aerial data were not smoothed because there was no evidence that the data contained estimation errors as did the ship data.

An estimate of density in the total area ($\hat{D}_c$) was calculated by combining the aerial inshore ($\hat{D}_i$) and ship offshore ($\hat{D}_0$) density estimates weighted by the relative sizes of the inshore (A_i) and offshore (A_0) areas as

$$\hat{D}_c = \frac{\hat{D}_i A_i + \hat{D}_0 A_0}{A_i + A_0}$$

The estimate of variance of $\hat{D}_c$ is

$$V\hat{a}r(\hat{D}_c) = \frac{A_i^2 V\hat{a}r(\hat{D}_i) + A_0^2 V\hat{a}r(\hat{D}_0)}{(A_i + A_0)^2}$$

RESULTS

Factors Affecting Density Estimates

Aerial Data

Density estimates for the aerial data in the inshore area during calm seas or with minimal sun glare were more than twice the estimates for data taken during rough seas or poor sun conditions (Table 1). Differences in estimators were even greater for sea state and sun glare interaction effects. These differences may have occurred because observers failed to detect trackline schools during poor conditions or because sea state conditions were spatially confounded with distance from shore. Therefore, these differences may be reflecting a decreasing onshore-to-offshore density gradient. This was investigated by partitioning the inshore aerial data into "coastal" and "offshore" bands for each Beaufort sea state (Fig. 3) and sun glare condition (Fig. 4). Sufficient data were not available in each band to stratify detection rates by each sun and sea state interaction category.

Sea conditions during the aerial surveys were rougher offshore than nearshore. More searching was done in the coastal band during low Beaufort states, whereas more searching was done in the offshore band at higher Beaufort states (Fig. 3). The rates of detecting dolphin schools were higher at each corresponding Beaufort state in the coastal band than in the offshore band (Fig. 5). The rates of detecting trackline schools were generally higher in the coastal band; however, these rates were based upon very few

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[9] A. Hohn, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. January 1985.

[10] Holt, R. 1984. Estimation of density of dolphin schools in the eastern tropical Pacific Ocean using line transect methods. Southwest Fish. Cent. Adm. Rep. No. LJ-84-32, 72 p. National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 1.—Estimates of school density made during all conditions and during calm and rough seas using aerial and ship data; estimates made during good and poor sun condition using aerial data. Estimates are made for data in the inshore, offshore and total areas. Estimates for all conditions were calculated using 1977 through 1983 data and estimates for sun and sea state conditions were calculated using 1979 through 1983 data. Estimates are also presented for data collected during an aerial experiment testing effects of sea state and sun glare.

Variable	Distance searched (km)	Number schools detected (n)	Density ($\hat{D}$) (schools/ 1,000 km^2)	SE (D)	CV (D)
Inshore area					
Aerial data					
all data	34,006	152	4.18	0.902	0.216
calm seas	8,920	70	8.48	2.198	0.259
rough seas	25,086	82	2.71	0.611	0.255
good sun	11,994	74	6.57	1.504	0.229
poor sun	22,012	78	2.87	0.505	0.176
calm-good	3,026	30	12.64	5.290	0.418
calm-poor	5,894	40	6.24	2.311	0.370
rough-good	8,967	44	4.29	1.202	0.280
rough-poor	16,118	38	1.78	0.460	0.258
Ship data					
all data	27,840	379	4.47	0.514	0.115
calm seas	8,008	170	7.32	1.259	0.172
rough seas	14,668	149	4.05	0.772	0.191
Offshore area					
Ship data					
all data	46,567	322	2.04	0.263	0.129
calm seas	4,623	72	4.91	1.414	0.288
rough seas	20,976	99	2.01	0.435	0.217
All areas					
Ship data					
all data	74,407	626	2.95	0.253	0.086
calm seas	12,631	242	6.53	0.991	0.152
rough seas	35,644	248	3.02	0.445	0.147
Holt (text fn. 10) aerial experiment					
calm-good	1,414	37	29.18	7.357	0.252
calm-poor	3,014	81	23.78	5.888	0.248
rough-good	1,886	42	39.42	8.193	0.208
rough-poor	5,467	103	20.16	4.513	0.224

schools (18 trackline schools in the coastal and 10 schools in the offshore band were detected). Lower offshore estimates for data recorded under the same Beaufort state were consistent with a decreasing onshore-offshore density gradient.

Within each band, sea state conditions were also spatially stratified because the lower Beaufort conditions occurred mostly in the nearshore and northern regions of each band (Fig. 3). Predictably, detection rates for all schools within each band declined as the Beaufort condition increased. Because of the large variability inherent in small sample sizes and spatial stratification of searching effort at the various Beaufort conditions, comparisons of rates of detecting trackline schools did not yield consistent trends. For example, within both bands, the trackline detection rate for Beaufort 2 conditions was larger than for Beaufort 1 conditions. In the coastal band Beaufort 5 conditions had higher trackline detection rates than Beaufort 4 conditions and rates for Beaufort 4 were higher than rates for Beaufort 3 (Fig. 5).

Searching effort for aerial data during good and poor sun conditions was also confounded with distance from shore (Fig. 4) and thus with sea conditions. Most good sun conditions (78%) occurred in the coastal band, whereas 59% of all poor sun

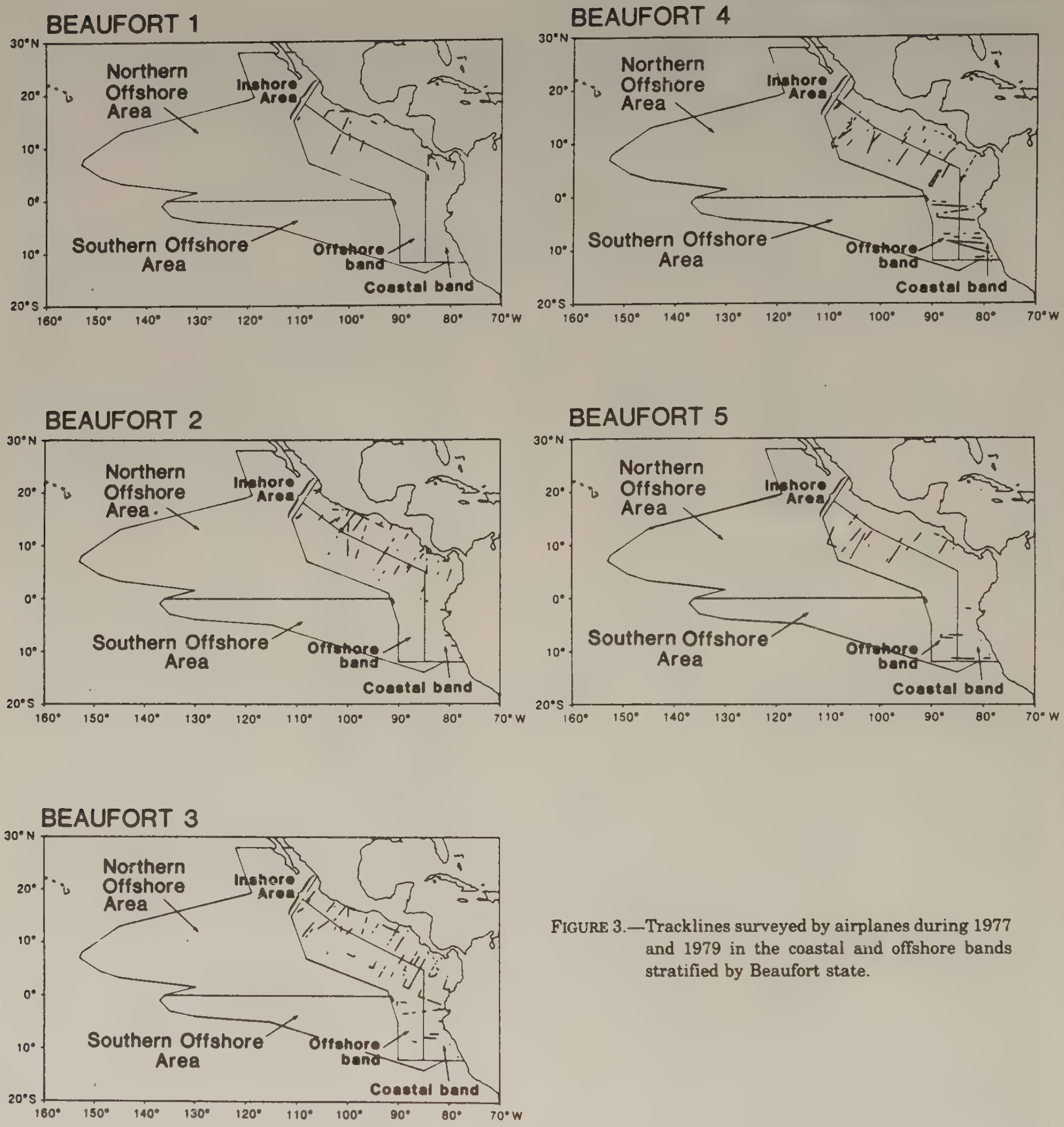

BEAUFORT 1
BEAUFORT 2
BEAUFORT 3
BEAUFORT 4
BEAUFORT 5
Northern Offshore Area
Inshore Area
Southern Offshore Area
Offshore band
Coastal band
30°N
20°
10°
0°
10°
20°S
160°
150°
140°
130°
120°
110°
100°
90°
80°
70°W

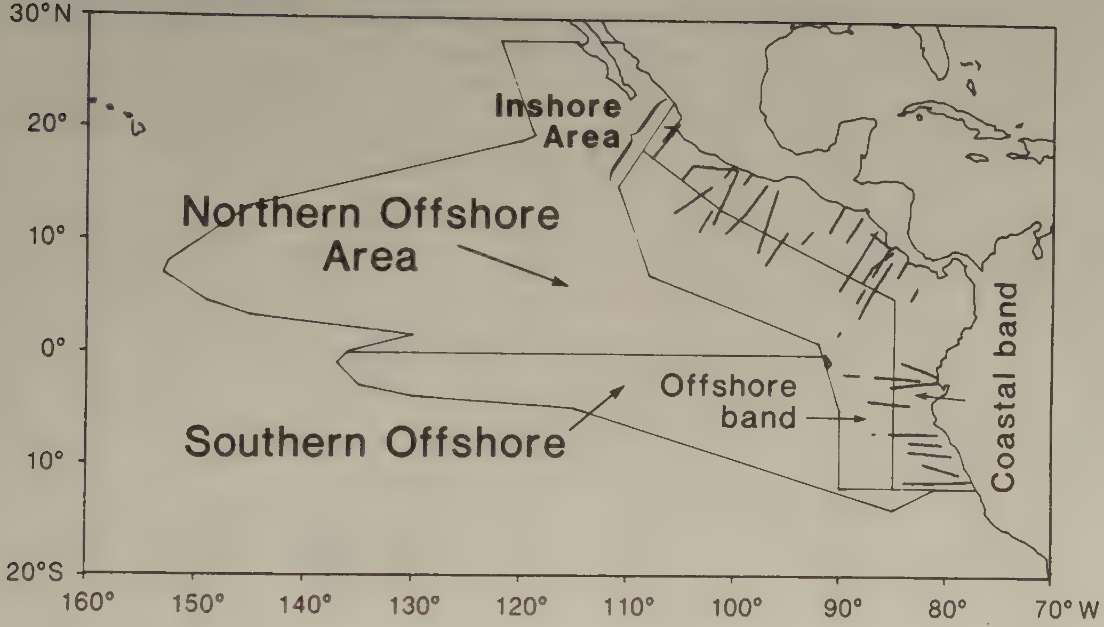
FIGURE 3.—Tracklines surveyed by airplanes during 1977 and 1979 in the coastal and offshore bands stratified by Beaufort state.

conditions occurred in the offshore band. This was because the general searching pattern was to begin searching on the westward, outbound leg in the morning, and then to turn the aircraft near noon and reach shore in late afternoon or night. Thus the sun was directly overhead or in front of the plane in the offshore reaches of the track and behind the plane in the nearshore areas.

Detection rates during good and poor sun conditions were higher in the coastal band than in the offshore band (Fig. 5), which was consistent with a hypothesized decreasing density gradient. Within the coastal band, detection rates during good sun conditions were greater than during poor sun conditions, but most of the poor sun data was gathered in the westward portion of the band (Fig. 4). In the offshore band, trackline detection rates during good and poor sun conditions were similar, but the rate during good sun conditions was based upon three sightings and only 8% of the effort.

Finally, I compared data collected by the ob-

A. GOOD SUN


30°N
20°
10°
0°
10°
20°S
160°
150°
140°
130°
120°
110°
100°
90°
80°
70° W
Inshore Area
Northern Offshore Area
Offshore band
Southern Offshore
Coastal band

B. POOR SUN

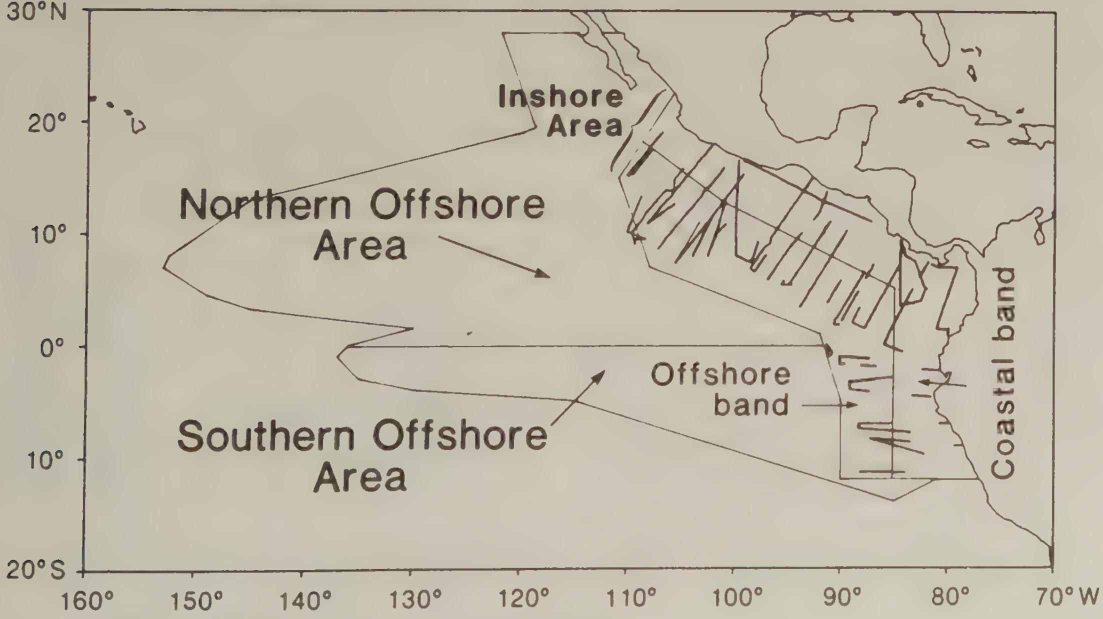

30°N
20°
10°
0°
10°
20°S
160°
150°
140°
130°
120°
110°
100°
90°
80°
70° W
Inshore Area
Northern Offshore Area
Offshore band
Southern Offshore Area
Coastal band

FIGURE 4.—Tracklines surveyed by airplanes during 1977 and 1979 during (A) good and (B) poor sun glare conditions in the coastal and offshore density bands.

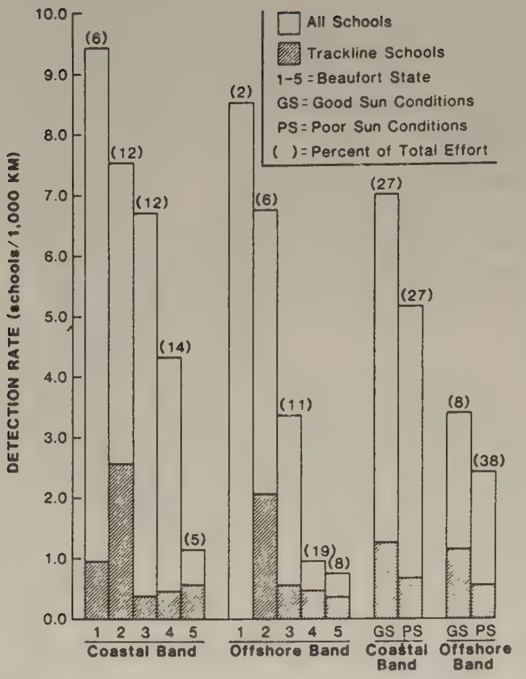


FIGURE 5.—School detection rates for aerial data in the coastal and offshore density bands for sea state and sun glare categories.

server teams to determine relative effects upon the density estimates. Team 1 and Team 2 searched approximately equal lengths of trackline (46% and 54% of the effort, respectively). No difference in performance of the two teams was evident: their rates of detecting schools, both on and off the trackline, and their estimates of school densities were approximately equal (Fig. 6).

Ship Data

The rates of detecting dolphins were greater during calm seas than during rough seas for the ship surveys from 1979 through 1983 (Fig. 7). The detection rate of dolphins during calm seas was more than twice the rate during rough seas in both the inshore and offshore areas. The ratio of calm sea to rough sea detection rates was larger in the offshore area than in the inshore area.

The offshore area was surveyed during rougher seas more than the inshore area (Fig. 8); seas were calm in the offshore area during only 17% of the effort as opposed to 35% for the inshore area surveys (Fig. 7). Dolphin density was lower offshore as indicated by lower offshore detection rates than inshore rates during either calm or rough seas (Fig. 7). The inshore-to-offshore-area detection ratios were 1.5 during calm seas and 2.0 during rough seas.

Sun glare had little effect on the shipboard estimates during either year because poor sun conditions occurred only during 6% of the 1982 and 8%

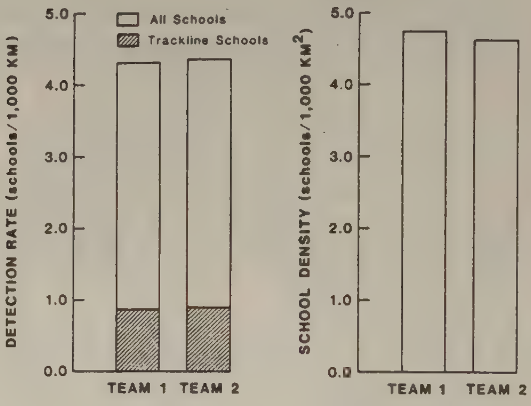


FIGURE 6.—School detection rates and density estimates for observer teams during the 1979 aerial survey.

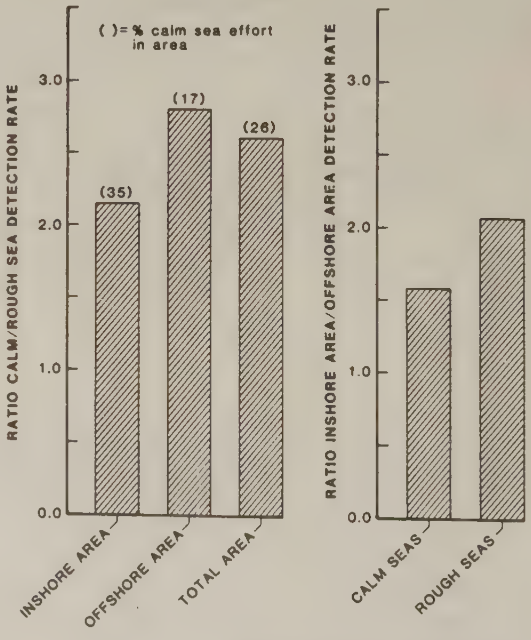


FIGURE 7.—Ratio of 1979-83 shipboard school detection rates for different sea states (calm sea versus rough sea) and area (inshore versus offshore). Detection rates computed with perpendicular distance data truncated at 2.1 km.

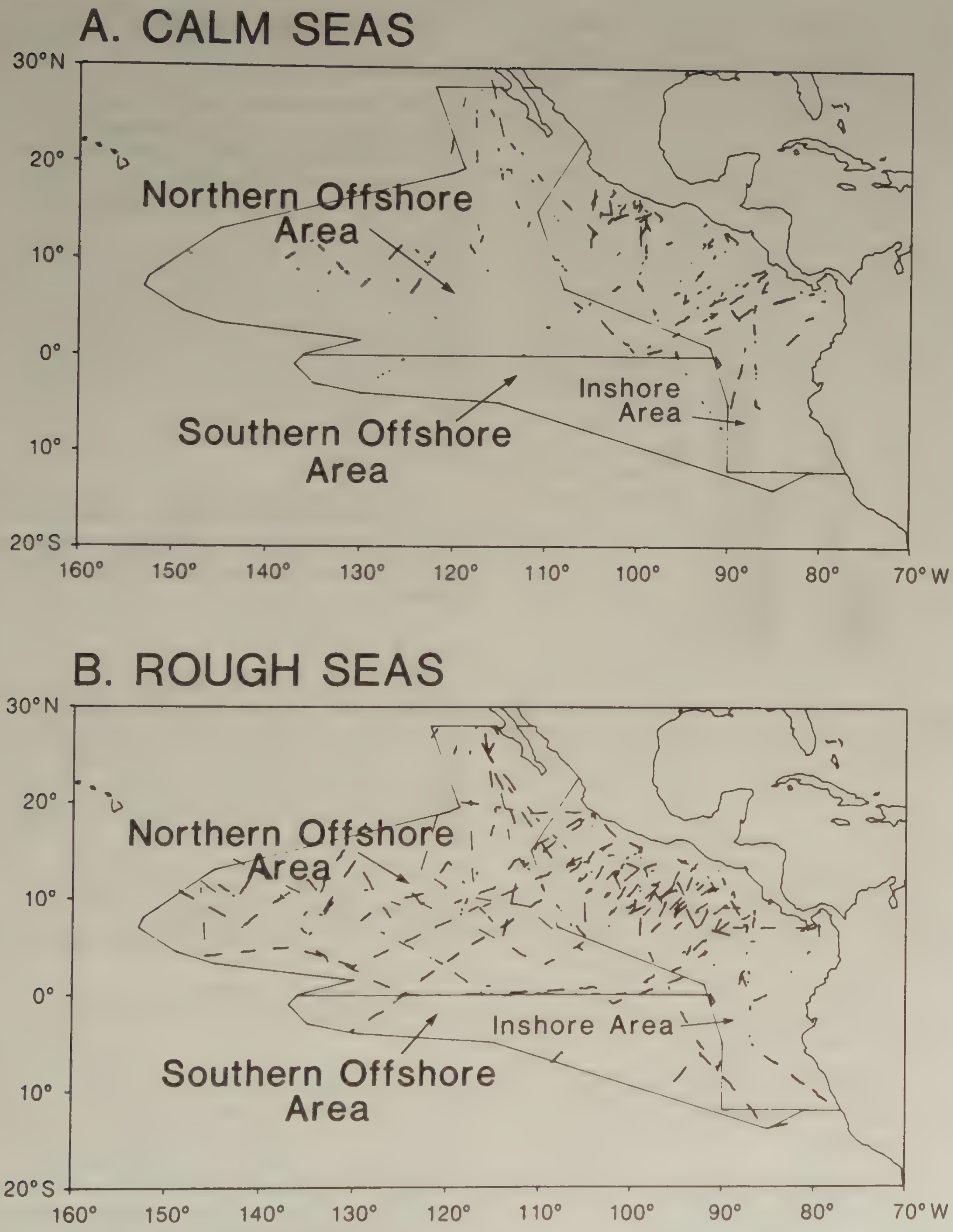

A. CALM SEAS
30°N
20°
10°
0°
10°
20°S
160°
150°
140°
130°
120°
110°
100°
90°
80°
70°W
Northern Offshore Area
Southern Offshore Area
Inshore Area
B. ROUGH SEAS
30°N
20°
10°
0°
10°
20°S
160°
150°
140°
130°
120°
110°
100°
90°
80°
70°W
Northern Offshore Area
Southern Offshore Area
Inshore Area

FIGURE 8.—Distribution of searching effort for the 1979-83 ship surveys during (A) calm and (B) rough conditions.

of the 1983 surveys. However, rates of detecting schools during good sun conditions were larger than during poor conditions (Fig. 9) and no schools were detected on the trackline during poor conditions.

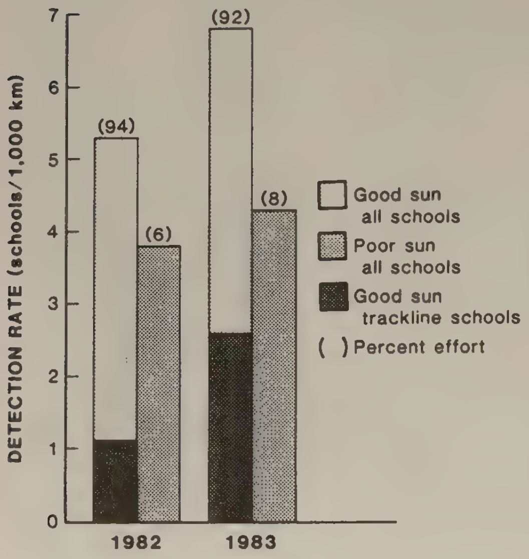


FIGURE 9.—School detection rates and relative density estimates during good and poor sun glare conditions for 1982 and 1983 ship data.

Density Estimates

Inshore Area

Aerial observers during the 1977 and 1979 surveys searched 34,006 km and detected 152 dolphin schools in the inshore area (Table 1). The estimate of school density using aerial data was 4.18 schools/1,000 km^2 with a standard error of 0.902.

From 1977 to 1983, shipboard observers searched 27,840 km in the inshore area and detected 297 schools (Table 2). Ship data yielded an estimate of density for the inshore area of 4.47 schools/1,000 km^2 with a standard error of 0.514 (Table 1). This was only slightly larger than the aerial inshore estimate.

Offshore Area

Observers aboard both vessels surveyed 46,567 km in the offshore area and detected 192 schools (Table 2). The estimate of density was 2.04 schools/1,000 km^2 with a standard error of 0.263 (Table 1).

Total Area

From 1977 to 1983, observers on both vessels searched 74,407 km in all areas and detected 489 schools (Table 2). The density estimate for all shipboard data was 2.95 schools/1,000 km^2 with a standard error of 0.253 (Table 1). The estimate of density using the aerial inshore estimate and the

TABLE 2.—School detection rates for 1977-83 ship data and for 1979-83 ship data stratified by sea state category in the inshore, offshore and total areas. Data were truncated at 2.13 km perpendicular distance.

Area/data source	Distance searched (km)	Percent (km) searched	Number schools detected	Percent schools detected	Detection rate (schools/ 1,000 km)	SE (detection rate)	Number days searched
Inshore area							
77-83 all data	27,840	100.0	297	100.0	10.67	0.82	173
79-83 calm seas	8,502	35.3	144	53.9	16.94	1.52	89
79-83 rough seas	15,609	64.7	123	46.1	7.88	0.92	124
Offshore area							
77-83 all data	46,567	100.0	192	100.0	4.12	0.50	251
79-83 calm seas	4,129	17.1	44	36.7	10.66	2.30	58
79-83 rough seas	20,015	82.9	76	63.3	3.80	0.56	134
Total area							
77-83 all data	74,407	100.0	489	100.0	6.57	0.47	417
79-83 calm seas	12,632	26.2	188	48.6	14.88	1.29	146
79-83 rough seas	35,624	73.8	199	51.4	5.59	0.54	256

ship offshore estimate was 2.71 schools/1,000 km^2 with a standard error of 0.334.

DISCUSSION

Onshore-Offshore Density Gradients

The onshore-to-offshore density gradient decreased based on aerial data in the inshore area and comparison of inshore and offshore density estimates. Offshore density estimates were only about one-half the inshore estimates (Table 1). Although sea state and sun glare conditions were confounded with distance from shore, comparisons of detection rates in the two inshore density bands for data stratified by Beaufort state or sun conditions indicated lower rates in the outer band (Fig. 5).

Fit of Fourier Series Model

Burnham et al. (1980) provided criteria for selecting the appropriate number of terms in the FS model. However, these criteria were not satisfactory for use with the aerial and ship perpendicular distance distributions, which had pronounced modes at the origin. Instead, I selected models which had the fewest terms but provided a good fit near the origin. This resulted in models with large numbers of terms. However, to the degree that the modes are representative of school density, my estimates of densities will be unbiased. Alternate statistical models need development which can fit data which lack a shoulder near the origin (i.e., data with pronounced modes at the origin). Buckland (1985) investigated several models but concluded that reliable estimation is not possible unless a shoulder exists.

Line Transect Assumptions

Aerial Data

Confounding of aerial sea state and sun condition data with distance from shore made it impossible to test the assumption that all trackline schools were detected during all viewing conditions. If viewing conditions had been homogeneous throughout the area, the density estimate calculated for calm sea and good sun conditions (12.64 schools/1,000 km^2) could be used for the inshore area (Table 1). This estimate is over 7 times the rough sea and poor sun estimate (1.78 schools/1,000 km^2). However, the calm seas and good sun condition effort occurred mostly in the northern nearshore region of the inshore area (Fig. 3, 4) where density may be high.

Consequently, Holt (fn. 8) conducted an aerial experiment in a relatively small area to test sea state and sun effects upon LT density estimates. The results indicated that sun glare adversely affected estimates of school density. The density estimate was 39% larger during good sun conditions than during poor conditions. Although density estimates were larger for calm sea data than for rough sea data, the differences were not significant.

The aerial experimental data (Holt fn. 8) may be used to estimate maximum bias for sun and sea state effects. The adjusted density estimate ($\hat{D}_A$) is

$$\hat{D}_A = \sum_{i=1}^{2} \sum_{j=1}^{2} \hat{D}_{ij} P_{ij} \left(\frac{\hat{D}'_{11}}{\hat{D}'_{ij}} \right)$$

where $\hat{D}_{ij}$ = Density estimate in survey area during ith sea state and jth sun condition,

P_{ij} = Proportion of effort in survey area with ith sea state and jth sun condition,

D'_{ij} = Experimental density estimate during ith sea state and jth sun condition determined from Holt (fn. 8).

In addition, i equal 1 denotes calm sea states and i equal 2 denotes rough sea states, and j equal 1 denotes good sun conditions and j equal 2 denotes poor sun conditions. An estimate of the sampling variance (Var($\hat{D}_A$)) using the Taylor approximation method is

$$V\hat{a}r(\hat{D}_A) = \sum_{i=1}^{2} \sum_{j=1}^{2} P_{ij}{}^2 \left[\left(\frac{\hat{D}_{ij}}{\hat{D}'_{ij}} \right)^2 V\hat{a}r(\hat{D}'_{11}) + \left(\frac{D'_{11}}{D'_{ij}} \right)^2 V\hat{a}r(\hat{D}_{ij}) + \left(\frac{\hat{D}_{ij} \hat{D}'_{11}}{(\hat{D}'_{ij})^2} \right)^2 V\hat{a}r(\hat{D}'_{ij}) \right].$$

The adjusted inshore density estimate is 4.51 schools/1,000 km^2 with a standard error of 1.107. This is an 8% increase over the unadjusted estimate (Table 1). The adjusted combined estimate for the entire ETP was 2.81 schools/1,000 km^2 with a standard error of 0.152, a 4% increase from the unadjusted estimate.

Using the experimental results to adjust aerial estimates for sun glare (and possibly sea state), effects may be suspect because of differences in procedures followed and observational conditions encountered in the experiment and the surveys: 1) The wings on the aircraft used during the experiment were attached on the lower part of the fuselage, whereas wings on the 1977 and 1979 aircraft were attached to the upper part of the craft which allowed better lateral observation. 2) Procedures used to adjust for presence of sun glare during the surveys and the experiment differed. Observers during the surveys were instructed to stop searching if they believed conditions prevented their detecting trackline schools, but observers in the experiment searched during all conditions. 3) More rough seas were encountered during the surveys (74%) than in the experiment (62%). Also, more (46% as compared to 15%) of the surveys' total effort occurred at extreme Beaufort 4 and 5 conditions. Because of these uncertainties, I used the unadjusted density estimate to determine school densities.

Comparisons of the 1979 aerial observer teams' estimates did not indicate observers of either team missed dolphin schools on the trackline but both teams may have been equally affected by searching conditions. These results were consistent with results of the aerial experiment (Holt fn. 8) where comparisons of observer teams' performance also indicated no significant differences.

Ship Data

The density estimates calculated from calm sea data were larger than estimates calculated from rough sea data (Table 1). The difference was probably not due to missed trackline schools during rough seas. Schools on the trackline would probably be detected as the ship approached unless the schools avoided the approaching ship. In a ship-helicopter experiment Hewitt (1985) investigated the reaction of dolphins to survey vessels and found that dolphin schools only occasionally react to the approach of a vessel before they are detected by shipboard observers (1 of 12 schools).

The differences between calm and rough sea estimates may have resulted from actual differences in densities in areas surveyed during calm and rough sea states (Fig. 8). Another possibility is that estimation errors resulted from observers detecting schools at greater radial distances during calm conditions (mean radial distance was 4.16 km) than during rough conditions (mean radial distance was 3.55 km). Estimation of sighting angles and distances of schools at greater distances from the ship may have been less accurate and may have increased the probability of schools being erroneously recorded near or on the trackline.

Although sun glare was not shown to affect the shipboard density estimates, Cologne and Holt (fn. 7) found that shipboard observers tended to avoid searching areas with sun glare. However, because of the relatively slow speed of the ship and the dolphins and because sun glare at any specific time is usually concentrated in a small region of the observers' field of view, all regions may be observed without glare.

The occurrence of errors in angle and distance estimations may have positively biased shipboard estimates. An inordinate proportion of dolphin schools (25% of all schools) was recorded as being on the trackline. Smearing the perpendicular distance distributions helped alleviate the bias but may not have eliminated it.

Comparison of Aerial and Ship Estimates

The estimates of dolphin densities in the inshore and the total areas using only ship data were slightly larger than estimates which used aerial inshore data (Table 1). This is logical because ship surveys were designed to overlap with aerial coverage in the inshore area and to provide systematic coverage of the offshore area. Therefore, they spent disproportionately more of their effort in the inshore area compared to its relative size and, within the inshore area, they spent disproportionately more effort in the northern nearshore region (Fig. 1), which has relatively high dolphin density. Although the inshore area represented 31% of the total area, 37% of the ship's effort was in the inshore area. In addition, 61% of the inshore effort was in the northern inshore region which represented approximately 44% of the inshore area. During the aerial surveys a systematic survey of the inshore area was conducted. Therefore, the best estimates of densities in the inshore and total areas are estimates calculated using the unadjusted aerial inshore data.

Comparisons with Previous Density Estimates

Density of ETP dolphin stocks have been estimated previously (SWFC 1976[11]; Holt and Powers 1982). The methods I used to calculate estimates were similar to those used by Holt and Powers. Therefore, differences that they noted between their assessment in 1979 and the SWFC 1976 assessment are also applicable to comparisons between the SWFC 1976 assessment and this study. My estimates differ from the 1979 estimates in that mine include

1) schools where either the observers' "best" or "lowest" estimate of mean school size was more than 14 animals (the 1979 assessment included only schools with "best" estimates),
2) use of the 1977 aerial data in the inshore density estimate,
3) ship data collected in 1977, 1979, 1980, 1982, and 1983 (the 1979 assessment included only 1979 ship data),
4) investigation of aerial and ship data for effects of sun, sea state, and observer performance,
5) application of LT methods to ship data to calculate density estimates.

Density estimates calculated in this study were similar to those presented in the 1979 assessment (Holt and Powers 1982). My inshore and offshore estimates were 4.18 and 2.04 schools/1,000 km^2, respectively, with standard errors of 0.902 and 0.263. Holt and Power's estimates were 3.51 and 1.89 schools/1,000 km^2, respectively, with standard errors of 0.590 and 0.766.

CONCLUSIONS

LT methods were used on 1977 and 1979 aerial survey data to estimate dolphin density in the inshore area at 4.18 schools/1,000 km^2. LT methods applied to 1977-83 ship data yielded an estimate of offshore dolphin density of 2.04 schools/1,000 km^2. By weighting aerial inshore and ship offshore data by the respective size of the two areas, the total dolphin density was estimated at 2.71 schools/1,000 km^2.

I investigated differences among densities at different visibility conditions for aerial data, but results were inconclusive owing to confounding of the factors with density gradient (area from shore). Adjusting the data for sea state and sun conditions increased the inshore aerial density estimate 8% and the total density estimate by 4%.

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FACTORS AFFECTING LINE TRANSECT ESTIMATES OF DOLPHIN SCHOOL DENSITY

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Abstract: An experimental aerial survey of dolphins was conducted to investigate the effects of sea state, sun glare, cloud cover, and observer experience on line transect estimates of school density and detectability. Although estimates during rough seas were lower than estimates during calm seas, and estimates from inexperienced observer teams were lower than estimates from experienced teams, these differences were not significant. School density estimates during poor visibility conditions, due to sun glare or cloud cover, were 39% smaller than during good conditions. Therefore, aerial survey designs should position tracklines to minimize glare under and forward of the plane. If possible, sea-state conditions greater than Beaufort 3 should be avoided, and experienced observers should be utilized.

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Line transect theory has been used to estimate population densities of cetaceans (Leatherwood 1979, Leatherwood and Show 1980, Scott and Winn 1980, Hammond 1981, Smith 1981, Holt and Powers 1982, Hammond and Laake 1983, Hammond 1984, Cooke 1985, Hiby and Thompson 1985, Holt 1985). The valid use of line transect theory is based upon several requirements (Seber 1973, Burnham et al. 1980) that have been assumed to be true or to have minimal effect on the estimates. One requirement, often suspected of not being met for cetaceans, is that all schools are detected on the trackline during all sighting conditions encountered during the surveys (Scott and Winn 1980, Holt and Powers 1982, Leatherwood 1982, Basson and Butterworth 1984). The ability of observers to detect all schools on the trackline may be affected by sea conditions or poor visibility and by the abilities of the observers. These factors are often confounded with each other or with other variables. For example, surveys that traverse nearshore and offshore tracklines may encounter rougher seas offshore, but animal density may decrease offshore. Thus, sea-state effects may be confounded with actual density.

In this paper we present results of an experimental aerial survey for dolphins that investigated the effects of sea state, visibility conditions, and observer performance on detecting dolphins and on density estimates that were determined using line transect methods.

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METHODS

Line Transect Model

Density was estimated by the line transect method. Burnham et al. (1980) provide a thorough review of line transect theory, and, if all requirements are met, then the density of the dolphin schools can be estimated as:

$$\hat{D} = \frac{n\hat{f}(0)}{2L}, \tag{1}$$

where n is the number of sightings, L is the length of trackline searched, and $\hat{f}(0)$ is an estimate of the probability density function (PDF) with a perpendicular distance (distance from sighting to trackline) equal to 0. The sampling variance of $\hat{D}$ was estimated using the Taylor expansion (Seber 1973):

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Table 1. Number of transect segments classified by Beaufort sea-state conditions, in which from 0 to 6 sightings[a] of dolphins were detected/segment, Liberia, Costa Rica, 1981. Percents are of column totals.

No. of sightings/ segment	Beaufort condition[b]											
	1	%	2	%	3	%	4	%	5	%	Total	%
0	8	38	65	51	106	56	45	87	7	100	231	58
1	9	42	43	33	57	29	6	12			115	29
2	2	10	11	9	17	9					30	8
3	2	10	6	5	6	3					14	4
4			3	2	4	2	1	2			8	2
5												
6					1	1					1	0
Total	21		128		191		52		7		399	

[a] Segments with >1 sighting were pooled during analyses because relatively few segments had >1 sighting.
[b] Increasing number indicates increasing sea-surface roughness.

$$\widehat{\text{Var}}(\hat{D}) = \hat{D}^2\left[\frac{\widehat{\text{var}}(n)}{n^2} + \frac{\widehat{\text{var}}\,\hat{f}(0)}{(\hat{f}(0))^2}\right]. \qquad (2)$$

The variance of n was determined empirically as:

$$\widehat{\text{Var}}(n) = \frac{R\sum_{i=1}^{R}(n_i - \bar{n})^2}{(R-1)}, \qquad (3)$$

where $n = n_i/R$ with n_i denoting the number of schools observed on the ith trackline segment and R = total number of equal trackline segments. We used the average length of all effort legs (28.64 km) as the length of the trackline segments. Equal line segments for data in each stratum were formed by either partitioning effort legs or by summing contiguous parts of legs with identical conditions or whole legs until 28.64 km were searched. Use of Equation 3 is appropriate (Burnham et al. 1980) because the detection rates of trackline dolphin schools among the segments were not serially correlated ($r = 0.085$).

Several models have been used to estimate $\hat{f}(0)$ (Burnham et al. 1980). The Fourier series (FS) model was used in our study because, theoretically, the model could fit perpendicular sighting distributions of a wide variety of shapes. These included distributions with large numbers of sightings detected on or near the origin (trackline); i.e., "spiked" distributions.

The number of terms selected for the FS model was determined independently for data in each sea state, visibility, or observer-team stratum. Because the experimental objectives were to determine if schools were missed on the trackline during each stratum and to investigate these effects upon the density estimates, the number of terms used in the FS model was selected to provide the best fit of the data near the origin. Therefore, models were selected that had more terms than would have been selected using standard selection techniques (Burnham et al. 1980).

Experimental Design

The experimental survey was done from 7 March through 5 April 1981 near Liberia, Costa Rica, using a Beech AT11 aircraft equipped with a plexiglass nose cone. A study area was selected from the coast westward to approximately 86°40′W and from 11°N southward to about 9°30′N. During each flight, the plane flew at approximately 274 km altitude and 278 km/hour along systematically placed tracklines. Searching effort was recorded in time periods (effort legs) during which sea state, observability conditions, and observer positions were constant. A new effort leg was recorded when either of these conditions changed.

Dolphin species included in the data analyses were spotted (*Stenella attenuata*), spinner (*S. longirostris*), striped (*S. coeruleoalba*), Risso's (*Grampus griseus*), and unidentified dolphins. Data recorded for each school included species identification, estimate of perpendicular distance of the school from the trackline, observer who detected the school, and estimates of the school size. Dolphin schools with <15 animals were omitted because all animals of such schools may have been submerged at the same time, and thus not detectable, and because these species typically do not occur in small schools. Holt and Powers (1982) reported that schools averaged approximately 200 animals. The estimates of school size were not verified because the plane was not diverted to fly over a school that obviously contained >15 dolphins. Schools de-

Table 2. Estimates of parameters used in computing dolphin density ($\hat{D}$) for calm and rough sea conditions, during good and poor visibility conditions, and for experienced and inexperienced observer teams, Liberia, Costa Rica, 1981.

Variable	$\hat{D}$ (schools/1,000 km^2)	SE($\hat{D}$)	No. of line segments searched
All data	25.00	3.349	423
Sea state conditions[a]			
Calm	25.72	4.986	161
Rough	24.94	4.279	262
Visibility conditions[b]			
Good sun	34.83	7.112	120
Poor sun	21.15	3.692	303
Sea state–visibility interactions			
Calm sea–good sun	29.18	7.357	52
Calm sea–poor sun	23.78	5.888	109
Rough sea–good sun	39.42	8.193	68
Rough sea–poor sun	20.16	4.513	194
Observer teams			
Experienced	30.15	4.784	218
Inexperienced	20.52	4.177	205
Observer team–sea state interactions			
Experienced–calm sea	30.66	7.853	79
Experienced–rough sea	31.18	4.352	139
Inexperienced–calm sea	23.09	5.178	82
Inexperienced–rough sea	20.10	5.836	123
Observer team–visibility interactions			
Experienced–good sun	43.28	9.410	67
Experienced–poor sun	24.06	3.039	151
Inexperienced–good sun	24.09	9.800	53
Inexperienced–poor sun	20.08	4.773	152

[a] Calm = Beauforts 1–2 and rough = Beauforts 3–5.

[b] Poor = sun glare on trackline or cloudy skies and good = all other conditions.

tected at perpendicular distances >1.94 km (1.05 nm) were not used in the analyses.

Three observers searched for dolphin schools from observation positions aboard the aircraft: a bow station located in the nose cone and left and right stations located at the sides of the plane in the extreme aft of the cabin. The bow observer searched the region directly underneath the plane (the trackline or center area of the transect), while left and right observers searched areas from the edge of the plane outboard to a distance that varied with environmental conditions. A bow monitor, who occupied the bow station which is adjacent to the bow observer, had clear vision of the trackline to check the bow observer's performance in detecting schools. It was not possible to determine if the bow monitor missed schools detected by the bow observer because the bow observer upon detecting a school immediately indicated its location. Schools detected by the bow monitor were not included in the density comparisons because the bow monitor was not a member of the 3-member searching team.

Data were recorded for each Beaufort sea state (Bowditch 1966) and grouped into sea-state conditions without (Beaufort numbers 1–2) or with (Beaufort numbers 3–5) whitecaps. The presence of whitecaps was important because animal splashes were used as sighting cues during calm seas when whitecaps were present but were easily confused with whitecaps during rough seas.

Visibility effects were investigated by recording the horizontal and vertical position of the sun relative to the plane (Holt 1983). The bow observer periodically noted when sun glare was on the trackline during certain positions of the sun (Holt 1983). When sun glare was noted on the trackline at any time during the survey, visibility was classified as poor. During conditions when clouds obscured the sun, diminished light penetration into the water reduced an observer's ability to detect dolphins; therefore, visibility under these conditions was classified as poor. Visibility under all other conditions was classified as good.

Two methods were used to collect data on the observers' abilities to detect schools. First, the bow monitor provided a direct visual check of the bow observer's failure to detect trackline schools. When a school was detected by the bow monitor but was missed by the bow observer, the plane was turned to ensure that a school had been missed. Second, detection rates of an inexperienced team were compared to an experienced team. The 2 teams alternated searching at approximately 40-minute intervals.

Data Analyses

Statistical differences within and among sea state, visibility, and observer teams were investigated using estimates of the density of schools, $\hat{D}$ (schools/1,000 km^2). However, because the number of schools detected was insufficient to calculate density estimates for the interaction effects, the rates of detecting all (combined on and off the trackline) schools (schools/1,000 km searched) and the rates of detecting trackline schools (schools/1,000 km of trackline searched) were tested. Three-way analysis of variance (ANOVA) was used to investigate interaction effects; but, because of small sample sizes, 2-way ANOVA was used to compare density estimates under different sea-state and visibility conditions. Because sea-state effects were not significant, data were pooled over sea states and visibility conditions, and observer team effects on the density estimates were tested. Unless otherwise indicated, statistical significance was tested at the $P = 0.05$ level.

The application of the ANOVA models was modified (Appendix 1) because data were not sufficient to compute independent, replicate detection rates or school densities for each level of interaction of sea state, visibility condition, and observer-team strata. Instead, the mean density and variance (Equations 1 and 2) or mean detection rates were estimated for each level of interaction and used in the ANOVA model.

In addition to investigating sea-state effects using our calm and rough sea classifications, which were derived a priori, we investigated sea-state effects by comparing data among individual sea states (Beaufort states). These comparisons were made using 2 methods. First, ANOVA compared trackline detection rates of individual Beaufort data (Sea-State-5 data were omitted because they represented only 2% of the effort during which there were no sightings). Second, a nonparametric contingency table analysis compared the number of equal-length line segments with dolphin sightings vs. those without sightings (Table 1). This is equivalent to analyzing detection rates.

RESULTS

Sea-State and Visibility Effects

The estimate of school density with calm seas was slightly larger than the estimate with rough seas (Table 2) but the difference between the 2 estimates was not significant ($F = 0.003$, $P > 0.10$). Differences among trackline detection rates during individual Beaufort sea states were not significant ($F = 0.869$, $P > 0.10$). However, little effort during Beaufort 5 conditions existed, and detection rates during Beauforts 4 and 5 were lower than during Beauforts 1 through 3 (Fig. 1). In addition, Beaufort 3 trackline rates were higher than Beaufort 2 rates. The association between Beaufort state and proportion of segments with and without sightings was not significant for trackline sightings ($\chi^2 = 5.15$, $P = 0.161$) but was highly significant for all sightings ($\chi^2 = 26.35$, $P < 0.001$).

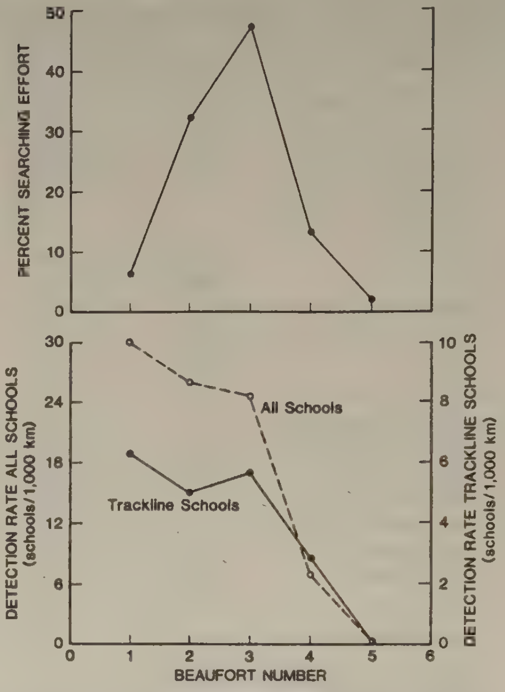

Fig. 1: Percent searching effort and detection rates of all schools and trackline schools of dolphins relative to sea state (Beaufort number), Liberia, Costa Rica, 1981. Increasing numbers indicate increasing sea roughness.

Density estimates of dolphin schools observed during good and poor visibility were 34.83 and 21.15 schools/1,000 km², respectively, and were statistically different ($F = 4.061$, $P < 0.05$). No significant interaction of visibility and weather effects on the density estimates was demonstrated ($F = 1.049$, $P > 0.10$). In general, density estimates during good visibility conditions were larger than during poor visibility conditions at each corresponding sea-state condition. However, the density estimate during good visibility conditions with rough seas was larger than during good visibility conditions with calm seas.

Observer Comparisons

Bow Monitor Comparisons.—During the experiment, bow monitors did not detect any large (>15 animals) dolphin schools on the trackline

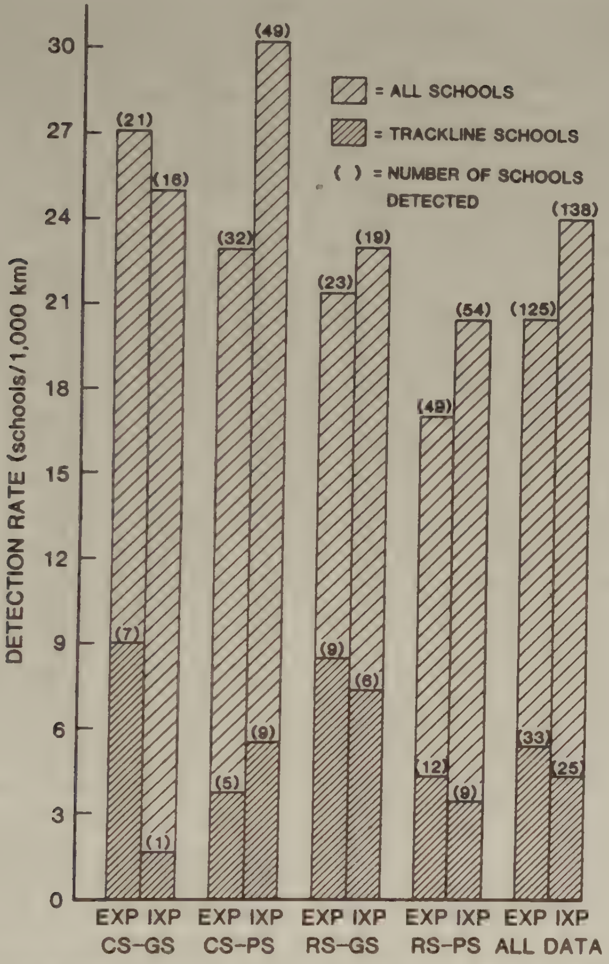

Fig. 2. Rate of detecting dolphin schools for perpendicular distance data for the experienced (EXP) and inexperienced (IXP) teams during calm sea–good visibility (CS-GS), calm sea–poor visibility (CS-PS), rough sea–good visibility (RS-GS), and rough sea–poor visibility (RS-PS) conditions, Liberia, Costa Rica, 1981.

that were missed by the bow observer. The only direct evidence that bow observers missed large dolphin schools on the trackline was the detection of 20 unidentified dolphins by the left observer. This school was sighted on the left boundary of the trackline in an area surveyed by both bow and left observers.

Observer-Team Comparisons.—Estimates of school densities were not statistically different between the inexperienced and experienced observer teams ($F = 2.497$, $P > 0.10$). However, the experienced team's density estimate was larger than that of the inexperienced team (30.50 vs. 20.52 schools/1,000 km^2, Table 2). Density estimates for the experienced team were larger than for the inexperienced team with calm sea conditions and with rough sea conditions (Table 2). Estimates of school densities were not statistically different for the 2 teams for good and poor visibility conditions ($F = 1.505$, $P > 0.10$). Estimates of school density for the experienced team were larger than for the inexperienced team during good visibility conditions and were slightly larger during poor visibility conditions (Table 2). The inexperienced team's estimates were similar with calm and rough seas and with good and poor visibility conditions. The experienced team's estimates were similar with calm and rough seas, but their estimate during good visibility was much larger than their estimate during poor visibility.

Neither consistent nor significant patterns were evident among observer-team detection rates, either trackline or all schools, for the various interaction effects with visibility and sea conditions. However, for either visibility condition, the detection rates of all schools for both teams were lower during rough than during calm seas (Fig. 2). Trackline rates for all categories and teams ranged from 1.56 to 9.04 schools/1,000 km. However, some categories had small sample sizes.

DISCUSSION

Observers were required to continue searching for marine mammal cues despite severe glare on the trackline or cloudy conditions that prevented visibility into the water. Bow observers frequently looked under and to the rear of the plane to avoid glare forward of the plane. Because the density estimate was 39% lower during poor visibility than during good visibility conditions, "acceptable" survey conditions must be rigorously defined prior to conducting future surveys.

The left observer's detection of a dolphin school on the trackline illustrated that bow observers missed some trackline schools. However, the detection of this school out of 265 total schools does not explain differences in the density estimates noted among the variables tested. In addition, bow monitors were subject to the same limitations as the bow observers.

The larger density estimate for the experienced team than for the inexperienced team was due predominantly to a relatively large estimate for the experienced team during good visibility conditions (Table 2). Density estimates were very similar for the experienced team under poor visibility conditions and the inexperienced team under good and poor visibility conditions. The relatively large estimate of density for the experienced team's good-visibility-condition data may be caused by: (1) incorrectly recording sightings near the trackline, as on the trackline by the experienced team during good visibility conditions so that estimates of $\hat{f}(0)$ were too large; (2) missing trackline schools by the experienced team during poor visibility conditions and by the inexperienced team during both good and poor visibility conditions; or (3) sampling error because of small sample sizes.

If incorrect data recording occurred for the experienced team during good visibility conditions, the rate at which schools in that stratrum were detected off the trackline should be correspondingly lower. However, the experienced team's good visibility and poor visibility off-track detection rates were approximately equal and were only slightly less than the inexperienced team's off-track detection rates during both visibility conditions (Fig. 3). It is possible, but not likely, that trackline schools were missed by the experienced team only during poor visibility conditions, whereas the inexperienced team missed schools during both visibility conditions. However, the estimate for the experienced team during good visibility conditions was based on a relatively small sample. (Only 16% [1,840 km] of the total searching effort and 17% of the total sightings were completed by the experienced team during good visibility conditions.)

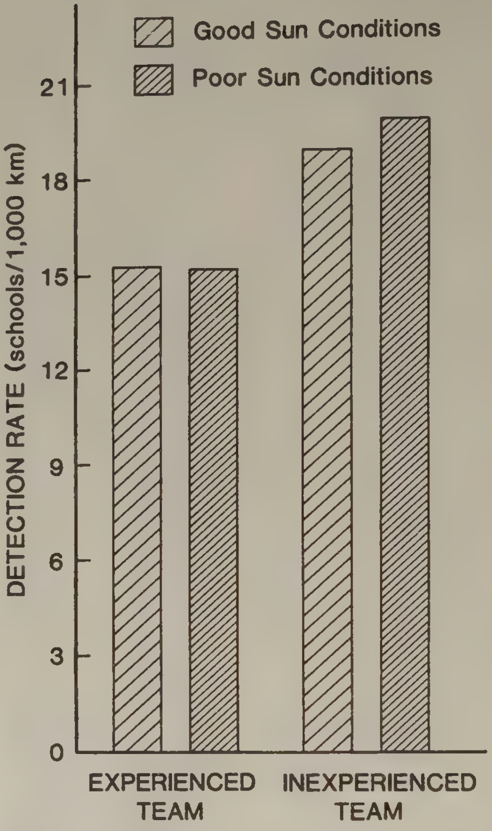

Fig. 3. Detection rate of dolphin schools off the trackline for experienced and inexperienced observer teams, Liberia, Costa Rica, 1981.

Erroneous differences among density estimates for variables being tested may result if the estimation models fit poorly or are applied inconsistently among data strata. We attempted to avoid these problems by ensuring that the models closely fit the sighting distributions near the origin. One indication of a model's performance is how well the pooling robustness criteria were met (see Burnham et al. [1980] for criteria development). Pooling robustness occurs when the sum of the density estimates of data in each stratum (such as calm- and rough-sea strata) equals the estimate of the total data set. The estimate for all data equalled 25.00 schools/1,000 km². Differences between this estimate and the sum of calm- and rough-sea-state data, the sum of good and poor visibility data, or the sum of experienced and inexperienced team data were not >0.66 schools/1,000 km².

Tracklines should be positioned to minimize glare under and forward of the plane. Sea conditions at ≥Beaufort 4 should be avoided during a survey. In addition, observer experience may not be critical, but the experienced team's estimates were consistently larger than those of the inexperienced team. Because operational and viewing conditions during our survey may not be consistent with conditions of other surveys, we caution against using our survey to correct for differences in other surveys.

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APPENDIX 1

A problem common to many studies of animal abundance is that a large effort must be expended to compute a single estimate of abundance with acceptable precision. Unfortunately, factorial experiments are often limited by resources to 1 estimate of animal abundance/cell in a multifactorial design. If the abundance estimate is approximately normally distributed, then the usual ANOVA method for a factorial design with 1 observation/cell may be applied; however, this is not a powerful procedure because of lack of replication in the individual cells, and testing interactions, except for the special conditions of Tukey's 1-degree-of-freedom test (Scheffe 1959), are not possible. In addition, the 1 observation/cell analysis ignores information about the variability of the abundance estimates. The following describes a method to analyze the factorial design to make use of within-cell variability.

If true replicates exist, the empirical estimate of the variance of an estimated density is (Burnham et al. 1980):

$$\widehat{\mathrm{Var}}(\hat{D}.) = \frac{\sum_{r=1}^{R} l_r(\hat{D}_r - \hat{D}.)^2}{(R-1)\sum_{r=1}^{R} l_r},$$

where $\hat{D}$ is the average over all replicates ($r = 1, \ldots, R$). If line lengths are equal ($l_1 = l_2 = \ldots = l_r$), then:

$$\widehat{\mathrm{Var}}(\hat{D}.) = \frac{l\sum_{r=1}^{R} (\hat{D}_r - \hat{D}.)^2}{L(R-1)}$$

$$= \frac{\sum_{r=1}^{R} (\hat{D}_r - \hat{D}.)^2}{R(R-1)}, \qquad \text{(A1)}$$

because $R = L/l$, where $L = \sum_{r=1}^{R} l_r$. Equation (A1) is the square of the standard error of $\hat{D}$.. Because the sum of squares within a single cell of an ANOVA table is the sum of squared deviations of the individual replicates about the cell mean, or

$$SS_{\text{error}} = \sum_{r=1}^{R} (\hat{D}_r - \hat{D}.)^2,$$

the error sum of squares within a cell may be obtained from the variance of $\hat{D}$. (Equation A1) as:

$$SS_{\text{error}} = R(R-1)[\mathrm{Var}(\hat{D}.)], \qquad \text{(A2)}$$

where R is the number of replicates in the cell of the ANOVA table and $\hat{D}$. is the cell mean. Therefore, if there were replicated densities, ANOVA tests could be performed using cell means and variances in lieu of individual density estimates.

When true replicates of density do not exist within each cell of the factorial design, the estimated density and its standard error, if statistically consistent, estimate the same quantities that the mean and standard error of the mean, respectively, would have estimated if true replicates were obtained. In this sense consistency is that the estimates would converge in theory to the correct values if complete enumeration were approached.

In the absence of true replicates, one must determine a value for the number of degrees of freedom (no. of hypothetical replicates minus 1) in each cell. This value cannot be arbitrary because it will affect both the size of the F-statistic and the critical level of the F-test through the number of degrees of freedom for error. We used the number of independent legs of effort searched as the degrees of freedom. Because Equation A2 assumes replicate lines are of equal length, we used a leg length equal to the average length of all legs in the study area.

We wrote routines to compute the ANOVA within- and between-group sums of squares and to compute F statistics for main effects and interactions. Because we had no control over the number of replicate tracklines in each cell in the analysis, we used weighted means formulas for the case of unequal *but proportional* cell sizes (Snedecor and Cochran 1967). If true cell sizes are not proportional, the weighted means analysis is only approximate. How good the approximation is for nonproportional cell sizes is not clear, but we believe the approximation improves with larger individual cell sizes.

RESEARCH VESSEL SURVEY DESIGN FOR MONITORING DOLPHIN ABUNDANCE IN THE EASTERN TROPICAL PACIFIC

RENNIE S. HOLT,[1] TIM GERRODETTE,[2] AND JOHN B. COLOGNE[3]

ABSTRACT

During 1986 the National Marine Fisheries Service began conducting long-term research ship surveys to determine status of spotted dolphin, *Stenella attenuata*, stocks in the eastern tropical Pacific. This is the main dolphin species taken incidentally by the yellowfin tuna, *Thunnus albacares*, purse seine fishery. We use research vessel survey data collected from 1977 to 1983 to investigate the annual changes in spotted dolphin population size that could be detected given various levels of research vessel survey effort during specified time periods for several levels of statistical error.

We find that two research vessels each operating for 120 days per year for 5 years (six surveys) could detect a 10% annual rate of decrease in dolphin abundance (a total 41% decrease over 5 years) with alpha and beta error levels of 10%. Adding a third vessel would provide better coverage of the dolphins' range, but would allow only a slightly lower rate of decrease to be detected (an 11% annual rate, for a total decrease of 44%). These numbers point out the difficulty of detecting even major changes in spotted dolphin population size with present survey methods. Alternatives are discussed, but all either cost more money, require a longer time to detect a decline, or accept higher levels of statistical error.

The National Marine Fisheries Service (NMFS) has the responsibility of determining the status of dolphin stocks which are taken incidentally by the yellowfin tuna, *Thunnus albacares*, purse seine fishery in the eastern tropical Pacific (ETP) (Richey 1976[4]). The status of spotted dolphins, *Stenella attenuata*, is of special concern since it is the major species taken by the fishery (Smith 1979[5]). Of the spotted dolphins, the northern offshore stock is of more concern since it has been fished more frequently than the southern offshore stock. The spinner dolphin, *S. longirostris*, and the common dolphin, *Delphinus delphis*, are also taken. In addition, the striped dolphin, *S. coeruleoalba*, and the Fraser's dolphin, *Lagenodelphis hosei*, are occasionally caught but are difficult to distinguish from the other three species at a distance (Holt and Powers 1982). These 5 species are herein termed target species.

The NMFS conducted assessments of population status in 1976 (SWFC 1976[6]) and again in 1979 (Smith fn. 5) based on estimates of *absolute* stock abundance. The validity of the absolute estimates depended on several assumptions being met. Unfortunately, some assumptions, such as not allowing systematic errors in data recording or the assumption that dolphin schools do not move prior to being detected by shipboard observers, may not have been met and thus the assessments were not entirely satisfactory. An alternative approach for assessing stock status, therefore, is to use *relative* population estimates to detect trends in stock sizes over a long time period. Relative estimates can provide an assessment of stock condition as long as the biases in the abundance estimates are consistent over the sampling period. Therefore, the NMFS is presently considering using annual estimates of population abundance as relative estimates to detect declines in population size of spotted dolphins during a sampling period of at least 5 years.

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[4] Richey, C. R. 1976. Memorandum of opinion. CA NO. 74-1465 and CA NO. 75-0227 U.S. District Court, District of Columbia, May 11, 1976.

[5] Smith, T. D. 1979. Report of the status of the porpoise stock workshop (August 27-31, 1979, La Jolla, California). Southwest Fish. Cent. Adm. Rep. No. LJ-79-41, 120 p. SWFC La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038

[6] SWFC (Southwest Fisheries Center). 1976. Report of the workshop on stock assessment of porpoises involved in the eastern tropical Pacific yellowfin tuna fishery. Southwest Fish. Cent. Adm. Rep. No. LJ-76-29, 60 p. SWFC La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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In this paper, we investigate the annual changes in the size of spotted dolphin populations that can be detected given various levels of research vessel survey effort within specified time periods. We investigate how many research vessels, assuming 120 days searching per vessel per year, would be required to survey the physical area inhabited by the major stocks. We also investigate how many vessels would be required to detect various levels of population declines in spotted dolphins during 5 years or, given fixed number of vessels, how many years of survey effort it would take to detect various population declines or, given fixed number of vessels for fixed number of years, the probability of detecting a decline (i.e., the power). We use historical data and current abundance techniques to predict variability of data which will be collected during the sampling period.

AREA INHABITED AND DATA SOURCES

For our analyses, the study area included the area described by Au et al. (1979)[7] as being inhabited by the target species (Fig. 1). The area north of lat. 20°N was excluded because spotted dolphins do not usually occur there. We partitioned the study area into four strata: the inside, middle, and west strata, which are located north of lat. 1°S, and a south stratum. The three northern strata were collectively termed the north area and all strata were termed the total area. In addition, a calibration area was defined as including part of the inside stratum (Fig. 1).

Data used in our analyses were collected from 1977 through 1983 by scientific observers aboard the NOAA ships *David Starr Jordan* and *Townsend Cromwell*. Survey coverage from the two ships for all years combined was thorough (Fig. 1). Data collected for each school included estimates of dolphin school size, species composition, and line transect observations, which we used to calculate density estimates.

SURVEY COVERAGE

We investigated the physical coverage of the area that is possible when using 1, 2, or 3 ships for

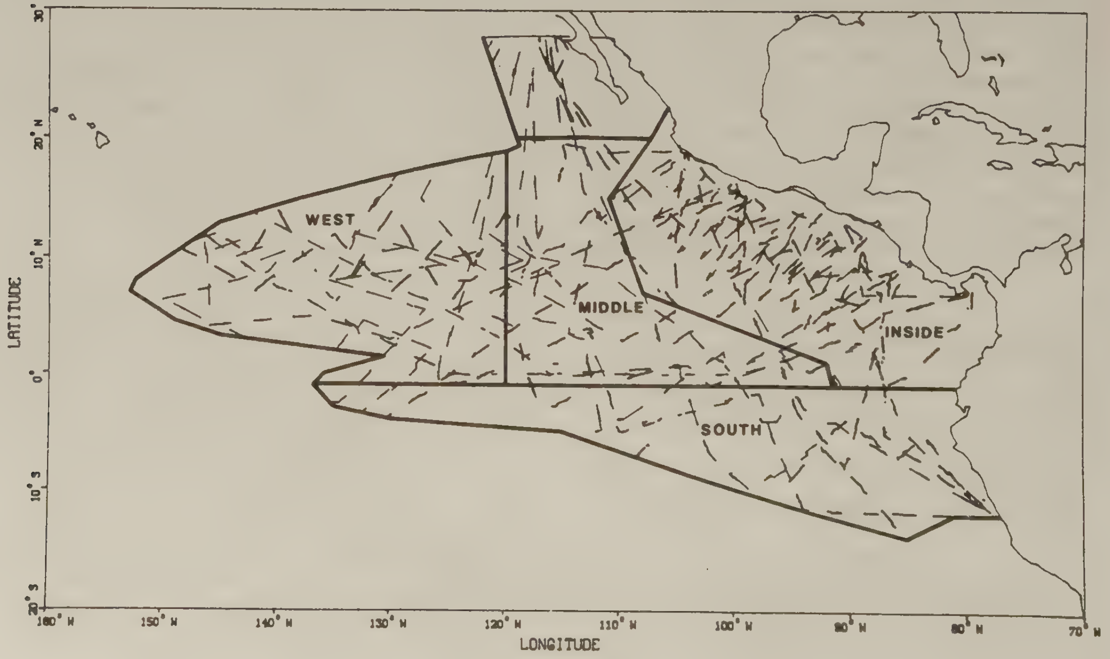

FIGURE 1.—Research vessel tracklines in each stratum during 1977 through 1983.

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[7] Au, D., W. L. Perryman, and W. Perrin. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. Southwest Fish. Cent. Adm. Rep. No. LJ-79-43, 59 p. SWFC La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

120 days each by plotting hypothetical tracklines. Approximately 370 km (200 nautical miles) of trackline could be covered in each survey day; with searching restricted to daylight hours, only about one-half of this distance would be searched. Approximately 40,700 km of trackline could be covered by each ship with less than 50% of this distance searched during daylight hours. Each ship's searching distance was allocated to each stratum by the square root of school density in the stratum. Effort of each ship was partitioned into 30-d segments between ports to meet logistical constraints of the vessels. We found that thorough coverage of the entire area was provided when three ships were used, two ships provided adequate coverage, and one ship provided very poor coverage with tracklines separated by large distances (Fig. 2).

DETECTION OF CHANGES IN POPULATION SIZE

Survey Design

The relationship among the number of samples, the rate of change, the precision of the population estimate, and the levels of alpha (type I) and beta (type II) statistical errors for several models of change and sample variability was investigated by Gerrodette (in press). We assumed that population size would change exponentially (constant rate per year). From Gerrodette's equation 15, using slightly different notation,

$$a(a+1)^2(a+2)[\ln(1-r)]^2 \geq 12(Z_\alpha + Z_\beta)^2 \sum_{i=0}^{\alpha} \ln\left[\frac{\mathrm{CV}_0^2}{(1-r)^i} + 1\right] \qquad (1)$$

where a = number of years in the survey period,
r = annual rate of decrease,
Z_α = percentile of standardized normal curve for one-tailed Type I error,
Z_β = percentile of standardized normal curve for Type II error, and
CV_0 = coefficient of variation of the population estimate at the present population size.

In this formulation, r is a positive number, and, since the first survey occurs at time 0, the total number of samples (i.e., number of annual surveys) is $a + 1$. Note that the null hypothesis is one-sided, namely, that spotted dolphin abundance is decreasing. In addition to the annual rate of decrease (r), the total population decrease which would occur over the entire survey period was calculated as

$$\text{Total decrease} = [1 - (1 - r)^a].$$

The survey design to detect changes in dolphin abundance was investigated in three ways. Using Equation (1), we computed 1) the minimum number of years (a), given one to three ships per year and 120 searching days per ship per year, required to detect various annual decreases in spotted dolphin abundance; 2) the minimum proportional annual change (r) that could be detected in 5 years given one to three ships per year at various levels of alpha and beta; and 3) power ($1 - \beta$) or the probability of detecting various decreases in population size in 5 years, given one to three ships per year.

To use Equation (1), the relationship of $CV(\hat{N})$, the coefficient of variation of the population estimate, and n, the number of schools detected must be determined. In addition, the rate per day at which dolphin schools are expected to be encountered must be known. We used the 1977–83 research vessel data to investigate these factors assuming these data would be representative of data that we will obtain during the proposed sampling period of 1986–91.

Abundance Estimation

Relative estimates of population abundance of spotted dolphins in the north and total areas were calculated using two methods, methods A and B. In method A, density and mean school size estimates were calculated in each stratum and abundance was determined (Holt and Powers 1982) as

$$\hat{N} = \hat{P}_t \sum_{k=1}^{m} \hat{D}_k \hat{S}_{tk} \hat{P}_k A_k. \qquad (2)$$

In method B, density and mean school size estimates were calculated for data pooled for the entire area (north area or total area) and abundance was determined as

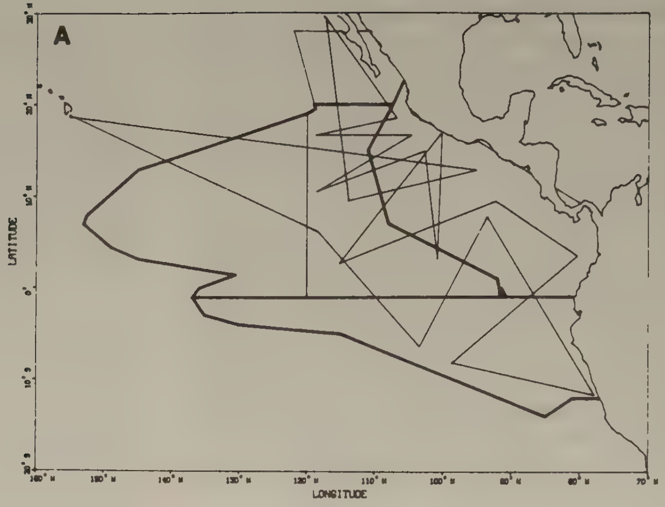


FIGURE 2.—Plot of hypothetical tracklines expected from use of one (A), two (B), or three (C) ships for 120 days each.

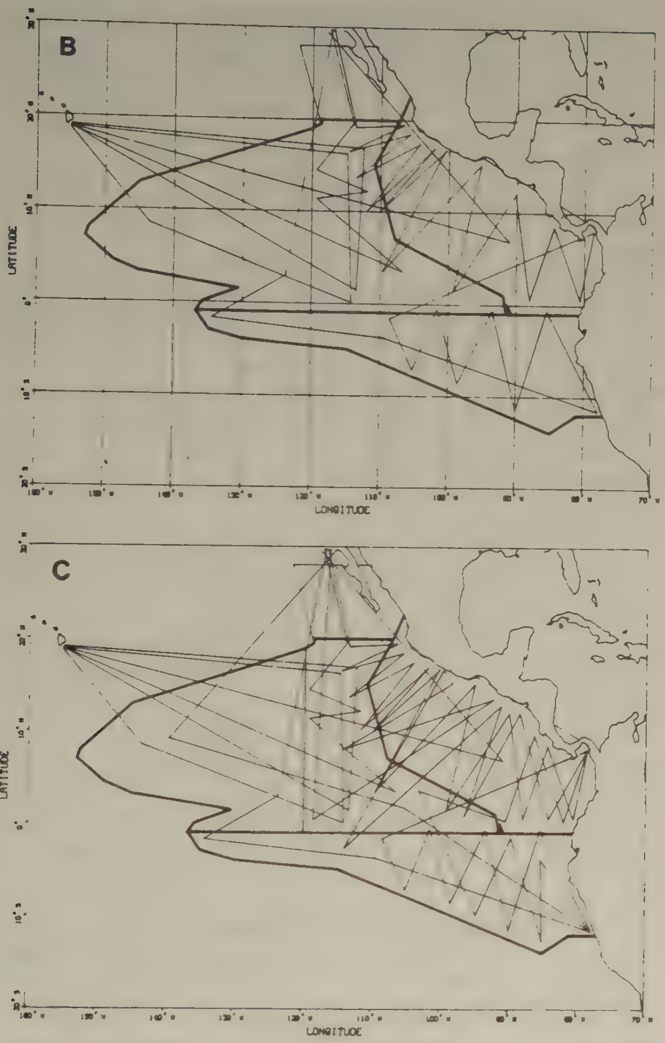
$$\hat{N} = \hat{P}_t \hat{D} \hat{S} \sum_{k=1}^{m} \hat{P}_k A_k. \tag{3}$$

where m = number of strata (3 for the north area and 4 for the total area),
k = 1, 2, 3, or 4 denotes the inside, middle, west, or south stratum, respectively,
$\hat{N}$ = estimated number of spotted dolphins in the survey area,
$\hat{D}$ = density estimate of number of schools of all dolphin species in the survey area (schools/1,000 km^2),
$\hat{D}_k$ = density estimate of number of schools of all dolphin species in the kth stratum (schools/1,000 km^2),
$\hat{S}$ = mean school size estimate for target species in the survey area (number of animals),
$\hat{S}_{tk}$ = mean school size estimate for target species in the kth stratum (number of animals),
$\hat{P}_t$ = proportion of all dolphins that were target species in the survey area,
$\hat{P}_k$ = proportion of spotted dolphins in the target schools in the kth stratum, and
A_k = area inhabited by all dolphins in the kth stratum.

The variance of $\hat{N}$ for Equation (2) was estimated using Taylor series expansion (Seber 1973) as

$$\begin{aligned}\hat{\mathrm{Var}}(\hat{N}) = \sum_{k=1}^{m} [&(\hat{S}_{tk} \hat{P}_t \hat{P}_k A_k)^2 \hat{\mathrm{Var}}(\hat{D}_k) \\ &+ (\hat{D}_k \hat{P}_t \hat{P}_k A_k)^2 \hat{\mathrm{Var}}(\hat{S}_{tk}) \\ &+ (\hat{D}_k \hat{S}_{tk} \hat{P}_k A_k)^2 \hat{\mathrm{Var}}(\hat{P}_t) \\ &+ (\hat{D}_k \hat{S}_{tk} \hat{P}_t A_k)^2 \hat{\mathrm{Var}}(\hat{P}_k)]\end{aligned} \tag{4}$$

The variance of $\hat{N}$ in Equation (3) was determined using Equation (4), but density and school size estimates that were calculated for the entire area



were substituted for the respective stratified estimates.

Specific formulae to estimate variables and associated theoretical variances in Equations (2) through (4) are from Burnham et al. (1980), Holt (1985,[8] in press) and Barlow and Holt (1986). Variances for estimates of school sizes and school densities were calculated using jackknife techniques (Miller 1974).

Since serial correlation among sampling units (days of effort) will yield biased estimates of standard errors using the jackknife method, we analyzed serial correlation of dolphin school detection rates among various combinations of successive days of effort. Analyses indicated that correlation was significant among successive single days but was not significant for periods of 2 or more days. Therefore, the data were grouped by 2-d increments for the jackknife analyses.

Estimates of spotted dolphin population abundance and values used in Equations (2) and (3) to calculate the estimates are presented in Table 1. CV ($\hat{N}$)s were smaller for estimates calculated using method B than for estimates using method A.

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[8] Holt, R. S. 1985. Estimates of abundance of dolphin stocks taken incidentally in the eastern tropical Pacific yellowfin tuna fishery. Southwest Fish. Cent. Adm. Rep. No. LJ-85-20, 32 p. SWFC La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 1.—School density of all dolphin schools, proportion of all schools which were target schools, mean school size of target schools, proportion of target animals which were spotted dolphins, area of each stratum, abundance and K values for spotted dolphins. SE and CV denote standard error and coefficient of variation, respectively. Methods A and B refer to different ways of pooling data on school size and density (see text).

	Stratum				Area	
Variable	Inside	Middle	West	South	North	Total
School density ($\hat{D}$) (Schools/1,000 km^2)	5.33	3.42	0.82	1.93	3.20	3.03
SE ($\hat{D}$)	0.87	1.13	0.30	0.39	0.54	0.51
CV($\hat{D}$)	16.3	33.1	37.2	20.2	17.0	16.8
Prop. target (P_t)[1]	—	—	—	—	0.775	0.775
Mean school size (S_t) (Number animals)	108.59	113.89	121.06	157.65	111.62	118.21
SE (S_t)	9.82	11.24	23.28	29.84	7.44	7.92
CV (S_t)	8.6	9.9	19.2	18.9	6.7	6.7
Area (km^2 $\cdot$ 10^6)	4.602	3.764	5.298	4.359	13.664	18.024
Prop. spotted (P_k)[2]	0.38	0.51	0.51	0.26	—	—
SE (P_k)[2]	0.039	0.048	0.048	0.085	—	—
Abundance and K Values						
Method A						
$\hat{N}$ (Animals $\cdot$ 10^6)					1.571	1.839
SE ($\hat{N}$)					0.283	0.294
CV ($\hat{N}$)					0.18	0.16
Sample size (n)					507	602
K					4.05	3.93
Method B						
$\hat{N}$ (Animals $\cdot$ 10^6)					1.761	2.081
SE ($\hat{N}$)					0.240	0.250
CV ($\hat{N}$)					0.14	0.12
Sample size (n)					507	602
K					3.06	2.94

[1]Source Holt (in press).
[2]Source Barlow and Holt (1986).

Relationship Between Var ($\hat{N}$) and Number of Schools Detected

In order to minimize the number of years required to detect a specific trend, Var ($\hat{N}$) should be as small as possible (Gerrodette in press). Var ($\hat{N}$) depends on the variance of the estimates of school size, school density, and proportions of the various dolphin species, as shown in Equation (4). Each of the variances of these estimates, in turn, depends on n, the number of sighted schools. Therefore, the dependence of Var ($\hat{N}$) on n must be known to calculate the number of sightings needed to attain a given level of precision (Var ($\hat{N}$)). We investigated the dependence of each of the individual variance terms on n.

Dependence of Var (S_{tk}), Var ($\hat{P}_t$), and Var ($\hat{P}_k$) on n

Because $\hat{S}_{tk}$ is the mean of n individual school size estimates, its variance is Var $(\hat{S}_{tk}) =$ Var $(S_{tk})/n$ where Var (S_{tk}) is the variance of school size. The Var $(\hat{P}_t) = P_t(1-P_t)/n$ where P_t is the true proportion of target schools among all dolphins. Var (S_{tk}) and $P_t(1-P_t)$ are both constant with respect to n, so Var $(\hat{S}_t) = O(1/n)$ and Var $(\hat{P}_t) = O(1/n)$, where $O(1/n)$ means "of the same order as $1/n$" and implies that as $1/n$ approaches zero, the variance approaches zero at the same rate. Similarly, Var $(\hat{P}_{ik})$, which is also a proportion, is equal to $O(1/n)$.

Dependence of Vâr ($\hat{D}$) on n

The Vâr ($\hat{D}$), based on replicate tracklines (Burnham et al. 1980), is

$$\widehat{\mathrm{Var}}\,(\hat{D}) = \hat{D}^2\left[\frac{\widehat{\mathrm{Var}}\,(n)}{n^2} + \frac{\widehat{\mathrm{Var}}\,[\hat{f}\,(0)]}{[\hat{f}\,(0)]^2}\right] \qquad (5)$$

where n is the number of sightings and $\hat{f}\,(0)$ is the estimate of the probability density function of perpendicular distances extrapolated to the trackline. First,

$$\hat{\mathrm{Var}}\,(n) = \frac{R \sum_{i=1}^{R} (n_i - \bar{n})^2}{R - 1}$$

where R is the number of replicate lines of equal length (l). For R of moderate size, $R \cong (R - 1)$. Thus

$$\hat{\mathrm{Var}}\,(n) = \sum_{i=1}^{R} (n_i - \bar{n})^2 = O(\mathrm{R}).$$

This is because $\hat{\mathrm{Var}}\,(n)$ is the sum of the variances of R independent values (n_i, $i = 1, 2, ..., R$) each having the same expected variance. But $R = n/E(n_1)$, the total number of sightings divided by the expected number of sightings for a line of length l. Thus, $R = O(n)$, and

$$\frac{\hat{\mathrm{Var}}\,(n)}{n^2} = \frac{O(n)}{n^2} = O(1/n). \qquad (6)$$

Second, $\hat{f}\,(0)$ was estimated using a Fourier series (FS) model (Burnham et al. 1980); therefore,

$$\hat{\mathrm{Var}}\,[\hat{f}\,(0)] = \sum_{j=1}^{m} \sum_{k=1}^{m} \mathrm{Cov}\,(\hat{a}_j, \hat{a}_k)$$

$$k = 1, 2, 3, ..., \textit{and } k > j > 1$$

where the a's are the coefficients in the series

$$\hat{a}_k = \frac{2}{nw} \left[\sum_{i=1}^{n} \cos \left(\frac{k \pi x_i}{w} \right) \right] = O\,(1)$$

with x_i equal the perpendicular distance to the ith sighting and w equal the truncation point for the perpendicular distance. Therefore, we only need to know the dependence of cov(a_j, a_k) on n. If n is much larger than one, $(n - 1) \cong n$ and

$$\hat{\mathrm{Cov}}\,(\hat{a}_j, \hat{a}_k) = \frac{1}{n-1} \left[\frac{1}{w} (\hat{a}_{k+j} + \hat{a}_{k-j}) - \hat{a}_j \, \hat{a}_k \right]$$

$$= O\,(1/n).$$

Since $\hat{f}\,(0)$ estimates a quantity which is constant with respect to n,

$$\frac{\hat{\mathrm{Var}}\,[\hat{f}\,(0)]}{[\hat{f}\,(0)]^2} = O\,(1/n). \qquad (7)$$

Combining Equations (6) and (7) with Equation (5), $[\mathrm{CV}\,(\hat{D})]^2 = O(1/n)$. This confirms discussions presented by Burnham et al. (1980).

In addition to investigating the theoretical dependence of $[\mathrm{CV}\,(\hat{D})]^2$ on n, we tested its empirical dependence on n using the research vessel data which included 479 days of survey effort. Data were truncated at 3.70 km perpendicular distance from the ship. Paired days of shipboard searching effort were randomly selected using a uniform random number generator until the number of associated sightings (n) equaled or exceeded a previously selected sample size. Sample sizes selected were 20, 30, 40, 50, 60, 80, 100, 200, 500, and 1,000. The resultant perpendicular distance distributions were smeared (a data smoothing technique described by Butterworth 1982, Hammond 1984, and Holt fn.8), and density, variance, and coefficient of variation estimates were calculated for each data set. The simulation was completed three times for each value of n.

The relationship between CV ($\hat{D}$) and $1/\sqrt{n}$ (Fig. 3) was linear ($F_{\text{lack-of-fit}} = 0.83$; $P = 0.59$) with intercept not significantly greater than zero ($t = 1.56$; $P > 0.10$). This confirms the analytical result above, that CV ($\hat{D}$) = $O(1/\sqrt{n})$; however, as n increased, the probability of randomly selecting data from each of the 240 pairs of days (479 survey days) multiple times increased which may

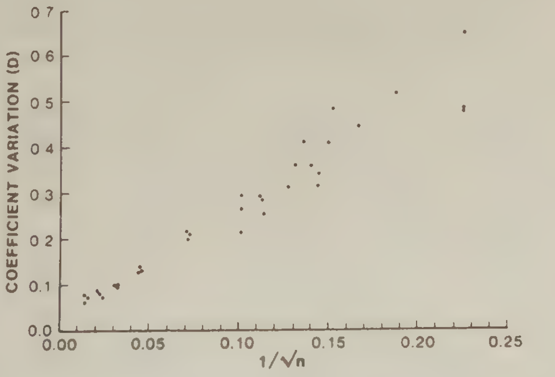

FIGURE 3.—Comparison of number of dolphin sightings (1/√n) and precision of the population estimate (CV(D)).

have biased CV $(\hat{D})$ if the distribution of sightings for the days were biased due to the effects of season or area. If we had included more large samples in our simulation, the linear relationship may not have been evident.

Calculation of K Values

Because all terms used to calculate Var $(\hat{N})$ equal $O(1/n)$ and Var $(\hat{N})$ is a linear sum of the terms, Var $(\hat{N}) = O(1/n)$ or CV $(\hat{N}) = O(1/\sqrt{n})$. Therefore, the relationship

$$\mathrm{CV}\ (\hat{N}) = K/\sqrt{n} \tag{8}$$

can be used to determine the change in CV $(\hat{N})$ for various values of n, where K is a constant. This relationship is true if the number of schools sighted is proportional to population size. This seems to be a reasonable assumption, although a more complicated relationship between density and school size, based on dolphin social structure and its interaction with the fishery process, is possible. K values for spotted dolphins in the north and total areas were calculated for methods A and B using the 1977–83 data (Table 1). These K values were then used to determine CV $(\hat{N})$s for specified values of n which would be expected assuming from one to three annual ship surveys.

Detection Rates

The number of expected sightings with use of one to three ships was calculated by computing detection rates as the average number of dolphin sightings per searching day. A day's searching effort generally consisted of searching from sunrise to sundown; therefore, we assumed most survey days covered approximately the same trackline distance. However, distance searched may vary inversely with rates of detecting dolphin schools because effort is halted so that observers can identify schools and make school size estimates. The number of survey days, and hence number of ships, required to obtain a specified CV $(\hat{N})$ was determined by dividing the number of required sightings by the rate of detecting schools.

Detection rates were caculated separately for data from the *Jordan* cruise and from the *Cromwell* cruise because of the wide disparity in detection rates of dolphins from the two vessels when operating simultaneously in the calibration area (Table 2). The *Jordan* has a much better platform from which to detect dolphins because its observation station was higher relative to the water and because the *Jordan* rode much smoother than the *Cromwell*. Pooled *Jordan* and *Cromwell* detection rates were calculated by standardizing the *Cromwell* rates to *Jordan* rates (Table 2) as

$$DR = \frac{R_j T_j + R_c T_c C}{T_j + T_c} \tag{9}$$

where DR = pooled standardized detection rate for all dolphin schools,

R_j = dolphin schools detected per day by observers aboard the *Jordan*,

R_c = dolphin schools detected per day by observers aboard the *Cromwell*,

T_j = days searched aboard the *Jordan*,

TABLE 2.—Detection rates of all dolphin schools from the *Jordan* and *Cromwell* in the calibration area and pooled standardized detection rates for both vessels combined calculated in each stratum. Standardized detection rates were calculated using the ratio of *Jordan* to *Cromwell* detection rates in the calibration area.

	Jordan (*J*)			*Cromwell* (*C*)			
Stratum/area	Number of schools (*n*)	Days searched (*D*)	*n*/*D*	Number of schools (*n*)	Days searched (*D*)	*n*/*D*	*J*/*C* ratio of detection rates
Calibration area	102	28	3.643	49	31	1.581	2.304
							Pooled standardized *n*/*D*
1. Inside	237	106	2.24	87	56	1.55	2.70
2. Middle	108	80	1.35	18	22	0.82	1.47
3. West	43	54	0.80	14	56	0.25	0.69
4. South	91	60	1.52	4	5	0.80	1.54
North area (Pooled strata 1-3)	388	226	1.72	119	128	0.93	1.87
Total area (Pooled strata 1-4)	479	282	1.70	123	132	0.93	1.84

T_c = days searched aboard the *Cromwell*, and

C = ratio of schools detected per day by observers aboard the *Jordan* in the calibration area during 1979 to schools detected per day by observers aboard the *Cromwell* in the calibration area during 1979.

The percent of searching days when one to three ships were used was allocated to each stratum (Table 3) by the square root of school density. The number of schools which would be expected to be detected based on the standardized detection rates then was calculated (Table 4).

TABLE 3.—Percent of searching days allocated by square root of density to each stratum in the north and total areas.

Stratum	North area	Total area
Inside	45.6	35.8
Middle	36.5	28.7
West	17.9	14.0
South	—	21.5

TABLE 4.—Number of days searched and number of schools detected per year of effort with use of 1, 2, or 3 ships allocated to the various strata by square root of density.

	North		Total	
Stratum	Number days	Number schools	Number days	Number schools
1 ship = 120 days				
Inside	55	149	43	116
Middle	44	65	34	50
West	21	14	17	12
South	—	—	26	40
Total	120	228	120	218
2 ships = 240 days				
Inside	110	298	86	232
Middle	88	130	68	100
West	42	28	34	24
South	—	—	52	80
Total	240	456	240	436
3 ships = 360 days				
Inside	165	447	129	348
Middle	132	195	102	150
West	63	42	51	36
South	—	—	78	120
Total	360	684	360	654

RESULTS

For either the north or total area, the same decrease in spotted dolphin populations can be detected 2 to 4 years earlier using method B, which uses pooled density and school size estimates, than when using method A, which uses estimates calculated for each stratum (Table 5). This is because large variances associated with the method A population size estimates occur due to small sample sizes in some strata. Therefore, method B was used in subsequent calculations.

The same number of years is required to detect a specific trend if the north or total areas are surveyed (Table 5). This result is true only if the 1977–83 data, which contain small sample sizes in the south stratum, are representative of future data. However, the northern offshore spotted dolphin stock occurs only in the north area and elimination of the south stratum will ensure better coverage of this north area, especially in the west stratum where sample sizes are minimal for applying the Fourier series model (Table 4). Therefore, subsequent calculations were made only for the north area. Annual population estimates for the northern stock would be biased only if substantial variation in the amount of dolphin migration between the north area and south stratum occurred during survey years.

TABLE 5.— Number of years required to detect an annual 5% decrease in spotted dolphin population size using 1, 2, or 3 ships and 2 different methods of pooling data. Method A utilized Equation (2) in text while method B utilized Equation (3). Alpha and beta levels equal 0.05, and effort was allocated to the various strata by square root of density. Number of schools expected to be detected each year determined using detection rates from Equation (9). K determined using Equation (8). CV ($\hat{N}$) denotes coefficient of variation of population abundance estimate.

Stratum	Number ships	Number schools	K	CV ($\hat{N}$)	Years required
North area					
Method A	1	228	4.05	0.27	17
	2	456		0.19	12
	3	684		0.15	11
Method B	1	228	3.06	0.20	13
	2	456		0.14	10
	3	684		0.12	9
Total area					
Method A	1	218	3.93	0.27	17
	2	436		0.19	12
	3	654		0.15	11
Method B	1	218	2.94	0.20	13
	2	436		0.14	10
	3	654		0.11	8

At the 5% error level, only rates of change of 11% per year or greater can be detected in a 5-yr survey period, even using three ships per year (Table 6). This is a rather high rate of decrease,

TABLE 6.—Minimum rates of annual decrease and minimum total decreases in spotted dolphin population size which could be detected in 5 years under different conditions. Changes were calculated for several alpha and beta levels, with a one-tailed test, using 1, 2, and 3 ships, for CV (*N*) determined using jackknife formulae, and data in the north area pooled over all strata (method B).

Number ships	CV (*N*)	Decrease per year	Total decrease
$\alpha = \beta = 0.05$			
1	0.20	0.19	0.65
2	0.14	0.13	0.50
3	0.12	0.11	0.44
$\alpha = \beta = 0.10$			
1	0.20	0.14	0.53
2	0.14	0.10	0.41
3	0.12	0.08	0.34
$\alpha = \beta = 0.20$			
1	0.20	0.09	0.38
2	0.14	0.06	0.27
3	0.12	0.05	0.23

and would lead to a 44% reduction in population size over the 5-yr period. If two or one ship is used, however, the minimum detectable rates of decrease are higher still, 13% and 19%, respectively. When the power of the survey design is considered, the same dilemma is evident (Table 7). Even when three ships are used, the power is acceptably high only if the rate of decrease is at least 10% per year. The probability of detecting a 5% per annum decrease at a 5% alpha level, for example, is only 0.51. This means that with a probability of 0.49 we would conclude that no decrease had taken place, when in fact it had. Power is even less if only one or two ships are used.

TABLE 7.—Power, or the probability of detecting a decrease in spotted dolphin population size during a 5-yr period. Power was calculated for surveys using 1, 2, or 3 ships, for various rates of annual and total population decrease, and for testing the regression of population size against time at various significance levels (α).

Number of ships	CV (*N*)	Rate of decrease per year	Total decrease	Power when $\alpha =$ 0.05	0.10	0.20
1	0.20	0.01	0.05	0.08	0.14	0.26
		0.03	0.14	0.15	0.25	0.41
		0.05	0.23	0.26	0.40	0.57
		0.10	0.41	0.62	0.75	0.86
2	0.14	0.01	0.05	0.09	0.16	0.29
		0.03	0.14	0.22	0.34	0.52
		0.05	0.23	0.42	0.56	0.73
		0.10	0.41	0.87	0.93	0.97
3	0.12	0.01	0.05	0.10	0.18	0.31
		0.03	0.14	0.27	0.40	0.57
		0.05	0.23	0.51	0.66	0.80
		0.10	0.41	0.94	0.97	0.99

Alternatively, we may have either to conduct the surveys for more than 5 years and/or relax the acceptable alpha and beta error level (Table 8). With three ships and 5% error levels, 5 years is sufficient to detect a 10% per annum decline, but 9 years are required to detect a 5% per annum decline and 13 years are required to detect a 3% per annum decline. For alpha and beta levels equal 0.10 or 0.20 and use of three ships, a 5% decrease can be detected in 7 or 5 years, respectively.

TABLE 8.—Number of years required to detect various annual decreases and total declines of spotted dolphins calculated for several alpha and beta levels using 1, 2, and 3 ships. CV (*N*)s were calculated using jackknife formulae and using data in the north area pooled over all strata (method B).

Number ships	CV (*N*)	Decrease per year	Number years required	Total decrease
$\alpha = \beta = 0.05$				
1	0.20	0.01	39	0.32
		0.03	19	0.44
		0.05	13	0.49
		0.10	8	0.57
2	0.14	0.01	30	0.26
		0.03	14	0.35
		0.05	10	0.40
		0.10	6	0.47
3	0.12	0.01	27	0.24
		0.03	13	0.33
		0.05	9	0.37
		0.10	5	0.41
$\alpha = \beta = 0.10$				
1	0.20	0.01	32	0.28
		0.03	15	0.37
		0.05	11	0.43
		0.10	7	0.52
2	0.14	0.01	25	0.22
		0.03	12	0.31
		0.05	8	0.34
		0.10	5	0.41
3	0.12	0.01	23	0.21
		0.03	11	0.29
		0.05	7	0.30
		0.10	5	0.41
$\alpha = \beta = 0.20$				
1	0.20	0.01	24	0.21
		0.03	11	0.29
		0.05	8	0.34
		0.10	4	0.34
2	0.14	0.01	19	0.17
		0.03	8	0.22
		0.05	6	0.26
		0.10	3	0.27
3	0.12	0.01	17	0.16
		0.03	8	0.22
		0.05	5	0.23
		0.10	3	0.27

DISCUSSION

Our analyses indicate that our ability to detect changes in the size of spotted dolphin populations in the eastern tropical Pacific is not very great without substantial long-term ship time. This is not surprising given the vast area of ocean inhabited by the dolphins and the low sighting rate from ships. We feel our results represent a generally accurate picture based on available data. However, the analyses must be qualified by noting that the data used to generate these results were accumulated during all seasons over 5 years. Data collected in the future will come from surveys conducted at the same time each year and may be less variable. In addition, more precise data gathering techniques or data fitting models may become available. If so, these factors would yield greater ability to detect lower rates of decrease, greater power, and lower required number of years. On the other hand, the estimates of expected variance have dealt with survey precision (measurement error) only. If environmental variability is important, data collected in future surveys may be more variable than we have calculated. In long-lived animals with many year classes contributing to reproduction, however, environmental variability will tend to be less important than survey imprecision (Gerrodette in press).

The selection of appropriate alpha and beta errors levels depends on one's perspective. An alpha error would occur if we concluded that a decrease in dolphin abundance was occurring when in fact it was not. It is therefore of interest to the tuna industry to minimize this type of error. A beta error would occur if we concluded that no decrease in dolphin abundance was occurring when in fact it was. It is in the interest of conservation groups to minimize this type of error. As is well known in statistical theory, however, there is a trade off between the two types of error, a decrease in one leads to an increase in the other. In our analyses we have balanced the two types of error by making alpha and beta equal. We have also used a range of equal alpha and beta levels (0.05, 0.10, and 0.20) to illustrate how choice of error level can affect sampling design. Higher tolerance of error leads to lower rates of decrease which could be detected in shorter times, but, of course, one is less sure of the conclusions reached. Thus the choice of acceptable alpha and beta levels to use in detecting changes in spotted dolphin population size is a management decision based primarily on social rather than statistical criteria.

At least two ships are required to provide representative coverage of the survey area. Although use of a third ship provides better coverage, it does not substantially improve detection of population decreases. For alpha and beta levels of 0.05, a 5% per year decrease can be detected in 9 years with use of three ships or 10 years with use of two ships (Table 8). For other alpha and beta levels, use of the third ship only increases our ability to detect specific decreases by about 1 year. Given the annual cost of each ship, it would be more cost-effective to conduct the surveys for an additional year using only two ships. Another strategy is to conduct surveys less frequently than annually. Gerrodette (in press) provides a numerical example of this approach. For parameter values appropriate to spotted dolphins, conducting surveys less frequently than annually (every second or third year, for example) could save substantial ship time, but more years would elapse before a trend was detected.

If a 5% annual decrease in population size occurred, the number of spotted dolphins killed would have to be large. Assuming a spotted dolphin population of 2.5 million animals (Table 1) and disregarding natural mortality and reproduction, approximately 125,000 animals would be killed each year. The estimates of all dolphins taken by the fishery during each of the last few years are only about 40,000 animals per year (Hammond and Tsai 1983). It may be unreasonable to expect annual decreases at the 5% annual level; rather decreases of 3% or 1% per year would be more reasonable. If so, two ships would require at least 14 years to detect the decline (Table 8).

Nonetheless, the number of dolphins actually killed may exceed 40,000 animals per year because dolphin mortality aboard the unsampled trips of U.S. and non-U.S. registered vessels, which is assumed to be similar to that on the sampled trips, may in fact be substantially higher. In addition, the effects of chasing and capturing dolphins several times per year are not estimated in our analyses.

Techniques and data are presented in our paper to determine the optimal number of ships and number of years required to detect decreases in spotted dolphin populations in the eastern tropical Pacific. However, these techniques are applicable to investigate the amount of effort and time required to monitor changes in any appropriate population index for any species where sufficient data exists or can be collected to determine reasonable estimates of coefficient of variation.

SUMMARY

Use of three ships provides excellent physical coverage of the eastern tropical Pacific dolphin area. Coverage using two ships appears adequate while use of one ship yields very sparse coverage.

Assuming alpha and beta levels of 0.05, use of two ships for each of 5 years will only allow us to detect a 13% annual decrease in spotted dolphin abundance. This means that the population could decline by 50% during the survey period before it could be detected. If three ships are used for 9 years, a 5% decrease per year could be detected.

Use of two ships instead of three only decreases our ability to detect specific trends by about 1 year. For alpha and beta levels of 0.05, use of two ships will allow detection of a 5% annual decrease in 10 years, instead of 9 with three ships.

The sampling period may be shortened if larger alpha and beta levels and larger annual decreases are acceptable. For alpha and beta levels of 0.10, use of two ships will allow detection of a 10% annual decrease after 5 years during which a 41% decrease in the population could occur.

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13.

Growth and Contraction of Domestic Fisheries: Hawaii's Tuna Industry in the 1980s

Linda Lucas Hudgins and Samuel G. Pooley

INTRODUCTION

Hawaii's commercial fishing industry is undergoing a rapid transition. New tuna fisheries are developing while the old leader, the skipjack tuna (*Katsuwonus pelamis*) fishery, has declined. The skipjack industry lost its international market with the closing of the Castle and Cooke cannery in 1984; at the same time its domestic market share shrank in response to competition from other local tuna fisheries. Furthermore, availability of the skipjack tuna resource around Hawaii apparently declined and fishing costs increased, further exacerbating problems for the industry.

This paper examines events that are restructuring the fishing industry in Hawaii. Particular attention is given to the effects on the skipjack industry of (1) the closing of the tuna cannery, (2) the changed availability of skipjack around Hawaii, (3) the increasing costs of fishing for skipjack, and (4) competition from other tuna species in the Hawaii fresh-fish market. The first three sections of the paper describe recent tuna fisheries developments in Hawaii. A section on marketing tuna in Hawaii follows. The last section discusses policy issues relevant to expansion of domestic tuna production.

SKIPJACK TUNA INDUSTRY AND CANNERY OPERATIONS

For almost 70 years the skipjack tuna industry was Hawaii's major commercial fishery, supplying 68 percent of the state's annual landings (over 4,000 tonnes on long-run average), 42 percent of its annual ex-vessel revenues ($4 million in 1986 prices), and almost 100 percent of its seafood exports.[1] In recent years annual skipjack production declined to approximately 1,300 tonnes, worth $2.7 million. This decline in total catches is shown in Figure 1. Pole-and-line skipjack now constitutes

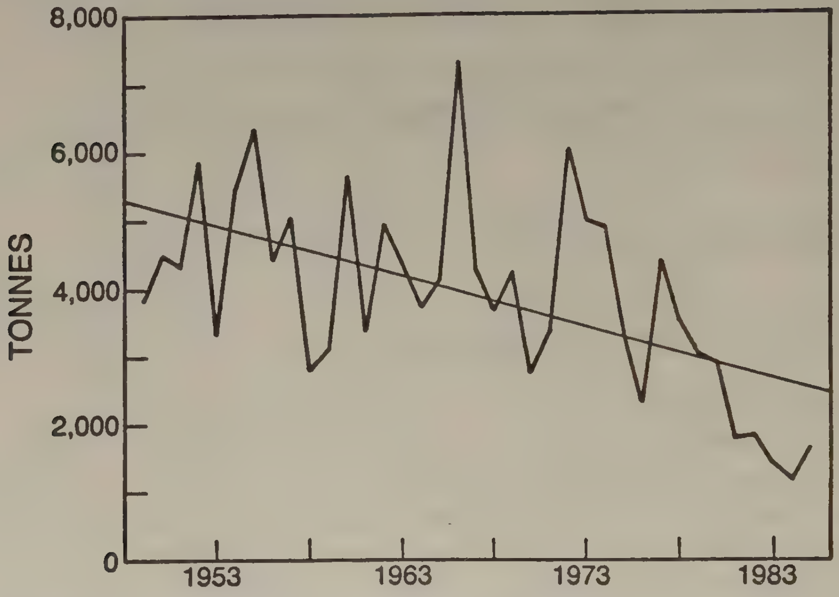

Figure 1. Skipjack tuna catch around Hawaii 1948–1983

Source: Skillman 1987.

about 22 percent of all tuna catches in Hawaii, down from a long-run average of 80 percent.

This fishery, known locally as the *aku* fishery, has existed since at least the turn of this century. Before World War II there were as many as 26 wooden-hulled vessels employing 300 fishermen using pole-and-line technology to fish with live bait for skipjack tuna. Over the years the skipjack fishermen have adopted only such minor technological advances as partial conversion to fiberglass poles. The vessels have crews of eight to ten and must forage for bait in Hawaii's harbors and bays before each trip. Today only eight vessels are actively fishing; one larger steel-hulled vessel is tied up waiting to be sold. Until 1984 the vessels sold both to the fresh market and to the tuna cannery; now they sell their catches entirely on the domestic fresh-fish market.

F. Walter Macfarland, a pineapple planter, founded Hawaii's tuna cannery, Hawaiian Tuna Packers (HTP), in 1917. He brought fishermen from Japan, built two gasoline-powered sampans, and signed five of the then-existing sailing sampans to supply the cannery with tuna. This facility packed up to 100,000 cases by 1922 (Castle and Cooke, Inc. 1977).

The existing four-line cannery building was constructed in 1932 at Kewalo Basin, the major commercial fishing harbor in Honolulu. The U.S. military took over the entire fishing fleet during World War II and converted the cannery to production of airplane gas tanks. After World War II HTP purchased about half of all skipjack catches from the remaining bait-boat fleet (17 vessels) and imported frozen tuna to supplement these domestic catches, processing about 72 tonnes of canned tuna per eight-hour day. HTP marketed the canned product under the Bumble Bee and Coral labels. The cannery also turned out Figaro cat food, fishmeal, and solubles used as additives for cattle and poultry feed. It was the site of the only commercial ice plant on Oahu, with a production capacity of 77 tonnes of ice per 24-hour day and a cold storage facility with a capacity of 1,760 tonnes. HTP also managed a shipyard on its Kewalo Basin premises.

The cannery changed ownership several times from 1917 onward. Castle and Cooke acquired it after World War II and owned it in one form or another until closing it down in 1984 because of corporate cash flow difficulties.[2] In 1985 Castle and Cooke sold the cannery, without the shipyard, to a group of Hawaii investors, the WRAF Corporation, who intend to integrate the cannery into a marine-oriented tourist center.[3] Under conditions of the 40-year land lease with the State of Hawaii, the WRAF Corporation must use the premises for a "minimum one-line fish cannery and the manufacture, storage, and sale of ice. Other permitted uses include the sale of seafood products, beverages and fishing equipment, a seafood restaurant, and supporting facilities. The lessee must also purchase all excess tuna as defined in and required by the lease for the purpose of assisting the local fishing industry" (Honolulu Star-Bulletin 1986). Rental for the land is $111,600 for 1987 and $125,550 for 1988. For each of the next ten years the rent will be $242,000 or 6 percent of gross receipts, whichever is greater. The lease also requires an expenditure of at least $300,000 in capital improvements at the site.

Reopening the cannery, even on a smaller scale, is an important economic and political issue in Hawaii for several reasons. First, the cannery employed over 400 persons. Second, the loss of cannery sales cost the skipjack fleet at least $500,000 in annual sales. Third, the skipjack fleet receives lower prices for its fresh-market sales and has reduced its production levels in response to the loss of the cannery market. Last, loss of an outlet for surplus skipjack tuna destabilized prices on the domestic fresh-fish market. (These cross-price effects are discussed below in the section on marketing.)

Even if the cannery reopens, the Hawaii fleet in its current status is unlikely to be able to catch enough tuna to fully supply the cannery. A one-line cannery requires about 18 tonnes a day (4,000 tonnes a year) to operate at full capacity. The average skipjack vessel in this fleet historically caught about 275 tonnes per year. At this level of productivity, the maximum the nine-vessel fleet could produce is about 2,475 tonnes a year. However, these vessels would sell first to the fresh market (historically around 1,045 tonnes per year), leaving about 1,300 tonnes to sell to the cannery.[4] Using only the locally caught skipjack, the cannery would be operating at about 35 percent of capacity. It could, however, draw on frozen imports, summer surpluses of domestically caught yellowfin tuna (*Thunnus albacares*), and landings from the distant-water albacore (*Thunnus alalunga*) fleet for supplemental supply.

On the other hand, reopening the cannery could attract new investment into Hawaii's skipjack fleet, either traditional pole-and-line boats or vessels with new technology. If these new entrants expect to be able to sell on the domestic market, their catches would have to maintain the high standard of skipjack available through the existing pole-and-line technology. Any new vessel entering the skipjack industry would also face competition in the fresh market from other Hawaii tuna fisheries, which have grown rapidly over the past ten years. In summary then, closing the cannery forced investors in the skipjack industry to consider processing techniques and market channels that had been postponed by reliance on the cannery. If the cannery reopens, some of this investment may yet be undertaken and lead to increased production.

Long before the cannery closed, there was an apparent change in resource availability of skipjack tuna around Hawaii. During the same period, the 1970s, industry production costs also increased. Therefore the closing of the cannery in 1984 may have been only the culminating event that threw the industry into decline. These resource and cost issues are discussed in the next section.

SKIPJACK RESOURCE CHANGES AND PRODUCTION COST INCREASES

Since 1974 the size distribution of catches has shifted from larger skipjack to smaller skipjack, with no documented change in fishing patterns. Large-size tuna as a percentage of total catches dropped from 64 percent in the 1964–73 period to 36 percent in the 1974–82 period (Table 1). Because large fish command a higher price in both Honolulu's fresh markets and cannery markets, the changed size distribution directly affects fishermen's revenues. The change in size of fish caught is estimated to have cost the industry about $362,000 per year in sales (Hudgins 1986). The causes of this change in size distribution are not yet clear. It may be that fishing pressure elsewhere in the Pacific by purse seine vessels and/or in the Northwestern Hawaiian Islands by Japanese pole-and-line vessels has decreased the availability of skipjack to Hawaii fishermen or that biological factors have affected fishing productivity.[5]

Table 1. Average annual size distribution of skipjack tuna catches around Hawaii 1964–1982

Period	Percentages			
	Large[a]	Medium	Small	Extra small
1964–73	64.1	16.1	15.5	4.1
1974–82	36.3	23.2	28.3	12.0

Source: Hudgins 1986, 12.

[a] Large = over 6.8 kilograms.
Medium = 3.6 to 6.8 kilograms.
Small = 1.8 to 3.6 kilograms.
Extra small = under 1.8 kilograms.

Along with the changed size distribution within catches came a decline in total tonnes caught, resulting in a loss of an additional $1 million per year in sales. For example, during the peak fishing years 1970–78 skipjack catches averaged over 3,200 tonnes a year; by the 1980s total skipjack production had declined to 1,300 tonnes annually. This decline in catches can be attributed primarily to the changing availability of skipjack around Hawaii rather than to cost increases or attrition in the fleet (Hudgins 1986).

Production cost increases, however, also have reduced long-run earnings and profitability in the skipjack industry. Pole-and-line skipjack fishing in Hawaii is relatively high in cost because of such fixed expenses as insurance and a high labor component compared to, for example, purse seine operations elsewhere in the Pacific. By 1983 total costs for an average vessel in the fleet exceeded the revenues as catches declined. With no profits to invest, the fleet's capital base depreciated. As fixed input prices for repairs, insurance, and loanable funds rose during the 1970s, the residual crew share also declined. A rise of 95 percent in inflation-adjusted prices for skipjack tuna during the 1970s may have been the only factor permitting some vessels to continue operating in the face of increasing costs and declining catches.

All but one of the existing vessels are at least 40 years old and require regular maintenance, without which they cannot get insurance. (Insurance is required for entering U.S. government harbor areas to gather baitfish; thus inability to get insurance can put a vessel out of the fishery.) These types of fixed costs are about 20 percent of total costs. The cost picture is further complicated by the fact that the larger vessels have operating-cost problems whereas the smaller vessels have fixed-cost problems. If fuel costs, about 22 percent of total costs, continue to decline, the larger and/or better maintained vessels will benefit. Insurance will, however, continue to be a problem as rates continue to increase (Pooley 1987).

OTHER TUNA FISHERIES

While the skipjack vessels have been affected by the closing of the cannery and by rising costs and resource problems, the other tuna fisheries in Hawaii have begun to grow and become competitors in the fresh-fish market. Estimates of the production of these other tuna fisheries are shown in Figure 2 and Table 2. State of Hawaii statistics report that these other fisheries comprise 55 percent of commercial tuna landings, substantially greater than their share before 1979.

These fisheries are most easily classified by gear type: the longline fishery for yellowfin, bigeye (*Thunnus obesus*), and albacore tunas and other large pelagics; the small-scale handline and troll fisheries for yellowfin and bigeye tunas; and the distant-water fishery for albacore tuna. There is also a large recreational tuna fishery for which few data are available.[6]

The longline fishery for yellowfin and bigeye tuna, and more recently albacore tuna, was traditionally Hawaii's second-largest fishery, highly prized for sashimi. The number of longline vessels declined in the 1960s and 1970s but began to recover by 1980. The number of long-

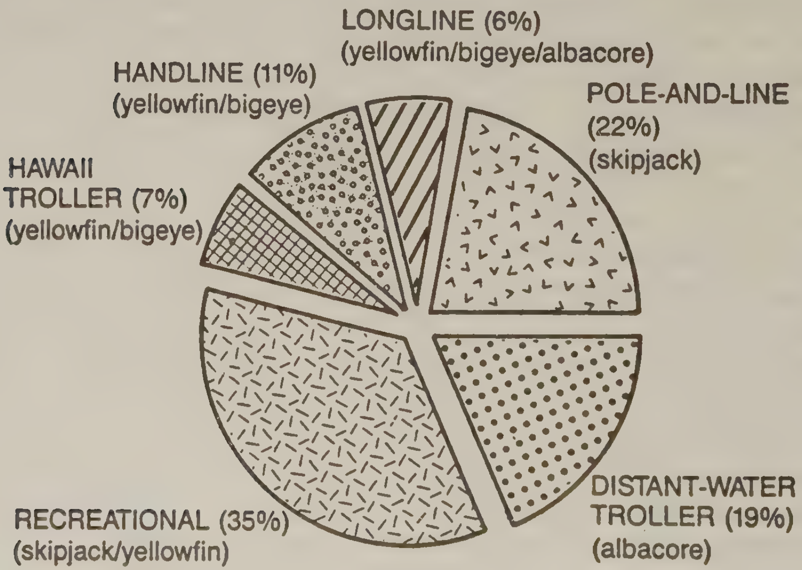

Figure 2. Estimated Hawaii tuna catches by fishery mid-1980s

Adapted from Table 2.

Table 2. Estimate of Hawaii tuna fishery production mid-1980s

Fishery*	Catch in tonnes	Value $m
Pole-and-line (skipjack)[a]	1,300	2.7
Longline (yellowfin, bigeye, albacore)[b]	370	1.7
Handline (yellowfin, bigeye)[c]	615	2.1
Hawaii troller (yellowfin, bigeye)[d]	410	1.1
Subtotal domestic commercial tuna landings	2,695	7.5
Recreational (skipjack, yellowfin)[e]	2,050	5.3
Distant-water troller (albacore)[f]	1,100	1.1
Total tuna landings	5,845	13.9

*This table shows *unofficial* estimates, presented to indicate relative magnitudes of production in Hawaii's tuna fishery. Because of inconsistencies in data reporting, the figures are estimated from the most accurate available sources, which are identified for each fishery. In some cases, only estimates based on knowledge of current operating characteristics could be made. Actual Hawaii Division of Aquatic Resources (HDAR) commercial tuna landings for 1984 were 2,745 tonnes valued at $6.5 million.

[a] Data are from HDAR 1985 monthly summaries (preliminary) and 1984 data by gear type.

[b] Data are extrapolated from HDAR 1984 total tuna landings for longline vessels, and reflect 2.86 X more boats reporting.

[c] Data are HDAR 1984 handline tuna totals for gear types 3, 8, and 9.

[d] Data are HDAR 1984 totals for tuna by gear type 6.

[e] Data are from unpublished National Marine Fisheries Service (NMFS) Marine Recreational Fishing Statistical Survey (MRFSS) results for 1981. Values are based on average commercial troll tuna prices in 1984. The MRFSS data have not been verified and are subject to significant variation.

[f] Data are based on one Hawaii trip per vessel, 60 short tons (54 tonnes) per trip, 20 vessels in the 1986 season. Values are current Honolulu delivery prices, which include transshipment discount.

liners operating in Hawaii today is difficult to determine. However, it is possible that the fleet has tripled since 1975 to approximately 40 vessels in 1986 (Honda 1987). There are also several multipurpose vessels that use longline gear during periods of peak tuna demand. Total catch for all these longline vessels could be as much as 370 tonnes per year ($1.7 million). These landings are marketed primarily on the Honolulu fresh-fish market and on the U.S. mainland. Bicatches of mahimahi (*Coryphaena hippurus, C. equiselis*), wahoo (*Acanthocybium solandri*), and various billfishes are sold in fresh-fish markets throughout Hawaii.

The fastest-growing fishery in Hawaii has been the tuna handline fishery (*palu ahi* and *ika shibi*) on the island of Hawaii. Using very small vessels (10 meters) and traditional fishing techniques, the fishery began with night fishing in the early 1970s. It grew to at least 200 vessels by 1981, then declined between 1981 and 1985. These small vessels can be very profitable because they have low operating and fixed expenses and because opportunity costs for labor are frequently low. This fishery is especially subject to fluctuations in the near-shore availability of tuna and to weather conditions that affect launching, recovery, and fishing effectiveness.

Annual catches of tuna—about 90 percent yellowfin—in the handline fishery could exceed 615 tonnes ($2.1 million). Most of the tuna is sold at the Hilo auction on the island of Hawaii, but some is shipped directly to the Honolulu auction or sold under contract for resale in Honolulu or on the U.S. mainland. Marketing has been constrained by a "burnt tuna" problem, which discolors the meat and substantially reduces its value. Nonetheless, handline-caught yellowfin, bigeye, and albacore tuna have become major competitors with skipjack in Hawaii's fresh-fish market.

There are also commercial and charter boat fleets that troll for tuna and sell on the domestic market; some recreationally caught tuna is also sold. Hawaii's commercial troll fishery supplies approximately 410 tonnes of tuna annually ($1.1 million).

The combined annual catches of Hawaii's non-skipjack tuna fleets, exclusive of the recreational catch, total approximately 1,400 tonnes ($4.9 million). Up to 25 percent of this catch may be exported directly to the U.S. mainland. The remainder—a substantial increase over the 1960s and 1970s—is sold on the fresh-fish market in Hawaii. Recreational catches, possibly the largest of all the fisheries, may exceed 2,000 tonnes annually (estimated value $5.3 million), but this is poorly accounted.[7]

Finally, a part of the U.S. distant-water albacore trolling fleet began using Hawaii as a seasonal base in the late 1970s. By 1982 some 75 distant-water albacore vessels (average size 20 meters catching about 40 tonnes per trip) were fishing the grounds above Midway Islands at the northern end of the uninhabited Northwestern Hawaiian Islands. Many of these vessels transited through Honolulu; some offloaded catch. However, with the decline of world tuna prices, the high salt content of brine-frozen products, and the closing of the Honolulu cannery, the cost of fishing in the central North Pacific became prohibitive for many vessels. Fewer than 25 vessels, 4 of them based in Hawaii, fished these waters in 1986. Total U.S. albacore catches in the central North Pacific in the mid-1980s (not all landed directly in Hawaii) were approximately 1,100 tonnes, valued at $1.1 million. New techniques, including flash-freezing, are being developed by some vessels to enhance fleet revenues. The albacore fleet is not expected to have an important impact on tuna marketing in Hawaii in the future, though it may provide an indirect benefit if vessels home-port in Honolulu or stop over for supplies. However, to the extent that some of these vessels make landings for the domestic fresh-fish market, there may be a substantial impact on bottomfish or pelagic markets.

As these other tuna fisheries developed, marketing practices became more sophisticated, extending outside Hawaii. Although no reliable estimates are available, it is probable that the growth of these fisheries, especially the handline fishery for yellowfin, affects prices and sales of skipjack in the market. Arrangements for marketing tuna in Hawaii are described in the next section.

TUNA MARKETING STRUCTURE

Annual seafood purchases of all species by Hawaii retailers for resale to the public are estimated to be $110 million (23,600 tonnes), with the population of Hawaii consuming twice the national average of seafood (Hudgins 1980b). Figure 3 indicates the source of Hawaii's retail seafood supply.

Tuna caught by Hawaii fishing vessels is about 2,800 tonnes (12 percent) of Hawaii retail sales. Hawaii vessels catching other pelagics and bottomfish provide about 5,900 tonnes (25 percent) to the retail sector

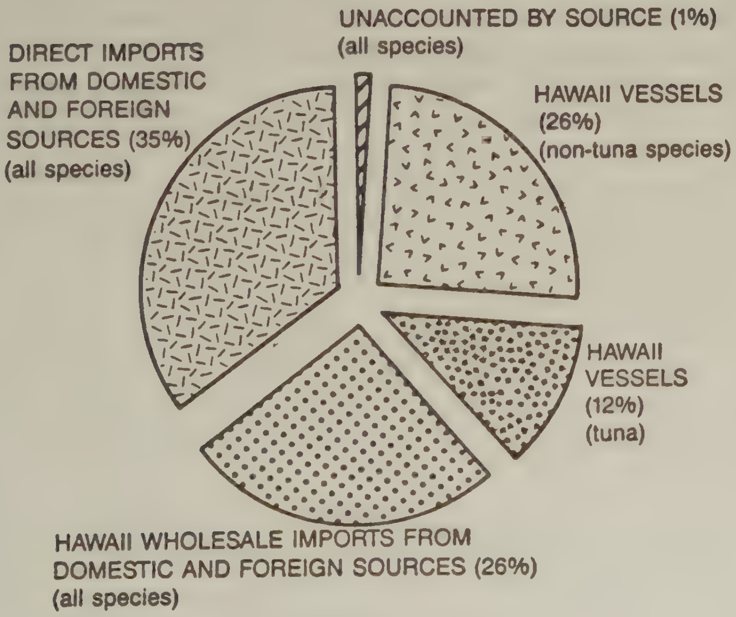

Figure 3. Hawaii retail seafood supply by source, percentage of total purchases (23,050 tonnes) 1983

Sources: Cooper and Pooley 1982; Higuchi and Pooley 1985.

for resale. Wholesalers provide about 6,100 tonnes ($23 million), 26 percent, from domestic and foreign overseas sources to local retailers for resale. The rest of the fish and seafood consumed in Hawaii, about 34 percent valued at $30 million, is imported directly from mainland U.S. suppliers or from foreign suppliers, with a small percentage coming from unspecified local sources (Cooper and Pooley 1982; Higuchi and Pooley 1985).

Much of this marketing is done through bilateral arrangements between wholesaler and retailer and is therefore difficult to examine directly. There are, however, two auctions and two fishermen's cooperatives that are central to marketing tuna in Hawaii. One auction, located near downtown Honolulu on Oahu, is expected to move to the new cannery complex; the other is in Hilo on the island of Hawaii. These auctions are markets for fresh large-size tuna and for bottomfish. (Only small amounts of skipjack pass through the auctions because skipjack is marketed primarily through the fishermen's cooperatives.) Wholesale dealers are the center of the auction system, which is based on the Japanese model of sale by individual large tuna and by individual lot of smaller fish. Both auction organizations have adapted to the times, welcoming a wider number of local buyers, assisting them in transactions with buyers and sellers from outside Hawaii, and promoting restaurant sales of fish to improve prices. The auctions also provide a number of functions to the commercial fishery (including short-term financing in some cases) which insure that the auctions maintain their centrality to the overall fish market.

Two fishermen's cooperatives have historically marketed skipjack tuna in Honolulu: the Tuna Boat Owners Association (TBOA) and the United Fishing Agency (UFA), which also runs the Honolulu auction. The cooperatives traditionally compete to supply the wholesale tuna market, which then resells to retail outlets. TBOA manages only skipjack vessels; UFA manages both skipjack and other vessels.

Before the cannery closed, TBOA vessels pooled their catches and determined shares of total sales revenues by formula. Each vessel's share was based on its contribution (weighted by size of fish caught) to the cooperative's total catch. The cooperative's sales manager allocated the fish between fresh and cannery markets to maximize revenues. When the cannery closed and membership in the cooperative declined, TBOA's role in marketing diminished, and the cooperative became more administratively oriented, handling such matters as providing health insurance and coordinating fuel and ice purchases for members. The strength of the cooperative was its ability to withhold a certain portion of the catch from the fresh market and sell it to the cannery, recognizing that other independent sellers of skipjack would be price followers. This action resulted in relatively high prices on the fresh market and higher revenues for the skipjack fleet as a whole. It was in the interest of both larger and smaller skipjack vessels to market cooperatively in order to maintain prices over time, as shown in Figure 4. The high-producing vessels, in particular, were able to make catches up to their capacity under the cooperative marketing arrangement and still capture a portion of the higher fresh-market price benefit.

As the range of tuna species available on the local market increased, marketing and market shares have become more important. Today, with the cannery closed, roughly 25 percent of total tuna catches are sold through the local fresh-fish auctions. Another 45 percent of the tuna catch is marketed by the cooperatives. The rest (30 percent) is marketed through contract arrangements between individual vessels and local retail outlets (restaurants and small grocery stores).

Price instability for all species in the fresh-fish market since 1984 is said to be a direct result of excess summer skipjack being put on the market during June, July, and August in competition with auction-sold yellowfin, bigeye, and albacore tuna. Reducing skipjack sales to the fresh market and selling the excess to the cannery would maintain prices on the fresh market. Price maintenance and an alternative sales outlet are especially critical in summer, when the large-size skipjack are caught. If the cannery reopens, a possibility to enhance revenues for the current skipjack fleet will exist in addition to more stability overall for fresh-fish sales.

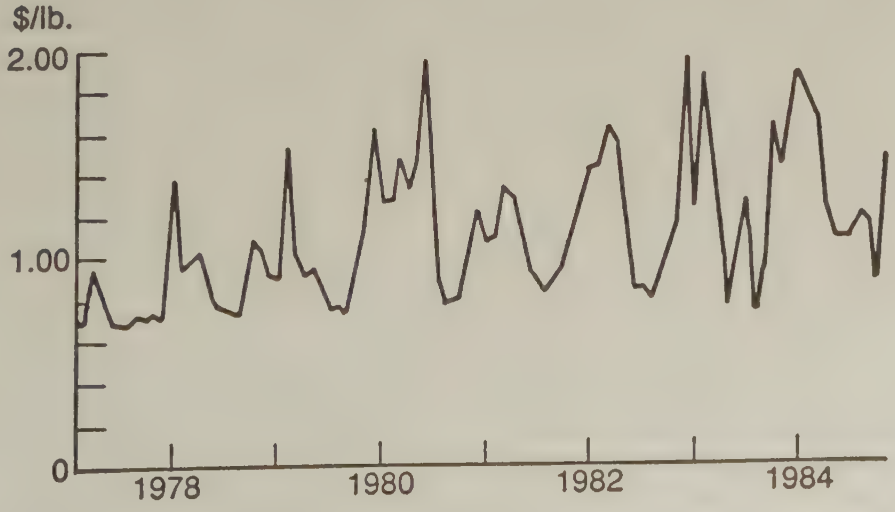

Figure 4. Monthly Hawaii fresh tuna market price trends 1977–1984

Sources: Hudgins (1980a) and unpublished industry data.

Sales of fresh tuna have become more fully integrated into one wholesale market for all tuna in contrast to the segmented markets that existed when the cannery provided an outlet for skipjack. Historically, there has been little observable cross-elasticity between skipjack prices and other tuna prices because the markets were not integrated. (Stronger cross-elasticities imply that the price of one tuna species is affected by the quantity sold of another.) With the restructuring of the skipjack industry so that more skipjack is sold in the fresh market, it appears that these cross-elasticities among tuna species have become stronger. The cross-price effects in the future may radiate throughout the entire fresh fish industry, resulting in losses to other than skipjack producers. Without the cannery sales for the pole-and-line skipjack fleet, all fresh-fish producers in Hawaii will face increased competition until the market stabilizes over the longer term.

INSTITUTIONAL CONSIDERATIONS

The commercial fishing industry in Hawaii is a small contributor to the state's overall economy, similar in scale to other products in Hawaii's diversified agriculture sector. Table 3 shows that locally caught seafood comprises as little as 0.1 percent of direct income to the gross state product, although the overall fishing industry, including a cannery, contributes more through processing, transshipment, and wholesesale/retail activities. Nonetheless, fishing is notable for the extent of its integration into Hawaii's social structure, the importance people place on access to fishing activities, and the perceived potential of fisheries expansion within the U.S. 200-mile zone.

Both the federal and state governments have encouraged fishery development projects, but most of the emphasis over the past ten years has been on non-tuna fisheries. Many in the fishing industry believe that government should play at most a facilitating role, leaving fishing operations and even fisheries development to private firms. Both U.S. and Hawaii governments have substantial fisheries research and development presences in Hawaii, but their application to tuna fisheries has diminished since the mid-1970s.

Although development of fisheries infrastructure was highlighted in the State of Hawaii Fisheries Development Plan (1979), the fiscal constraints of the U.S. government have substantially reduced the revenue-sharing grants available for harbor, launching ramp, and other fisheries developments. Despite this, Honolulu has generally adequate infrastructure facilities, and the increased movement of transient fishing vessels through the area—especially for the lobster, albacore tuna, and bottomfish fisheries—has increased the level of support available to

Table 3. Value of production in selected Hawaii industries 1983

	Value in $m	% of total value[a]
Sugar (including processing)	410	3.00
Pineapple (including processing)	219	2.00
Defense	1,848	13.00
Tourism	3,974	28.00
Flowers and nursery products	36	0.30
Aquaculture (raw product)	1	0.01
Commercial fishing (raw product)	10	0.07
Other agriculture (raw product)	115	0.80
Other primary industry and all secondary	7,739	54.00
Gross state product	14,352	100.00

Source: State of Hawaii 1985.

[a] Percentages do not add to 100.0 due to rounding.

local fleets. On the other hand, the limited access to launching ramps for small-scale commercial fishing boats and the unavailability of ice are significant constraints for fisheries development on the neighbor islands.

Other tuna industry problems include seafood quality and baitfish availability. The state's Seafood Product Promotion Committee, which has codified seafood availability, handling practices, and nomenclatures, has played a major role in improving tuna quality. Although considerable funds have been spent on baitfish research, including aquaculture facilities, only a pilot project on the island of Maui shows any near-term promise, and it may be terminated for lack of federal funding.

PERSPECTIVES ON THE TUNA INDUSTRY

The tuna industry in Hawaii is in a transition marked by changing production levels and developing market channels. The skipjack tuna industry has apparently suffered production declines because of the reduced availability of the resource and the closing of the cannery. At the same time, Hawaii's other tuna fisheries have expanded alternative markets for their fresh and frozen product, in particular through vigorous development of overseas markets. This expansion of market channels has had a salutary effect on the entire wholesale seafood industry in Hawaii and has assisted the development of the longline and handline tuna industries and the handline bottomfish industry.

However, the further development of domestic and overseas markets depends on three factors: the growth of the tourist market for seafood in Hawaii (6 million visitors per year), the increased availability of air cargo transportation between Hawaii and the overseas markets, and the modernization of marketing practices by Hawaii seafood dealers.

Despite the complexities and the transitional nature of these developments in the state's tuna fisheries, there is an important conceptual issue to be seen in Hawaii's case. That is, in order to increase production, a domestic fishery will at some point look to external market sales.[8] The development of canneries or sizable transshipment facilities may develop external sales and maximize value added from locally produced tuna, but risks attend such a development pattern. The external market (in Hawaii's case, the tuna cannery) appears to provide a stable outlet for surplus production. However, the external market itself is subject to international competitive price pressures and, in the case of a non-locally owned cannery, sales to the external market may depend on corporate decisions unrelated to the domestic industry. Conditions in the domestic industry and external dependence on the cannery both contributed to the transformation of the Hawaii skipjack industry in the 1980s.

If a fishery begins production on a small scale and expands to industrial scale to supply an external market, the two production levels are linked by the scale of the fishing fleet and by market interactions felt primarily in the domestic seafood sector. Industrial development may not involve a smooth transition from one level of production to another. Production at the output level required for an international commercial market implies more capital investment and higher fixed costs and therefore less flexibility in the face of changing production or market conditions. To amortize this larger investment, the fishing fleet will need to produce at near-full capacity and have a reliable sales outlet for its catch. Large-scale investment undertaken in response to *potential* sales in the externally linked market could lead to collapse of the industry if it must rely solely on domestic sales. In this event the higher-cost vessels would become marginally profitable while their catch of larger volumes of fish would jeopardize the economic well-being of the smaller vessels in the domestic fleet.

An important corollary issue obvious from the Hawaii skipjack industry case is the consideration of not only the degree of capitalization of the fleet relative to available markets but also the type or scale of capitalization. The skipjack industry in Hawaii, although contracted, will survive, precisely because it is based on small-scale technology. When the Hawaii cannery closed, the skipjack industry could either have moved to a lower long-run level of production or collapsed completely. The actual outcome depended on the type of technology adopted by the Hawaii industry over the years. As it was, the pole-and-line technology is relatively small in scale, and although there will be some attrition if the cannery remains closed, a portion of the fleet will remain to supply the domestic market for fresh skipjack whether the cannery reopens or not.[9] The remaining vessels will be those with relatively lower costs. If the technology had been larger in scale, and therefore dependent upon cannery sales, the cannery's closing might have brought about the complete failure of the skipjack fleet in Hawaii. Had the fleet had distant-water capabilities, the cannery's closing might have led to its deployment elsewhere in the Pacific.

It is difficult to assess the relative impacts of the many events that led to the restructuring of the fishing industry in Hawaii: closure of the cannery, decreased availability of the resource, increased production costs, and competition in the market from other tuna fisheries. The future of the skipjack industry is clearly tied to developing new market outlets for surplus production, maintaining fresh-market revenues, and containing costs. The future of the whole tuna industry in Hawaii will depend on continuing to pursue new markets as well as fulfilling current market demands with high-quality fish.

NOTES

1. Data are from unpublished monthly summary reports on commercial landings from the Hawaii Division of Aquatic Resources (HDAR).
2. In 1956 Bumble Bee Seafoods traded 12 percent corporate interest to Castle and Cooke in exchange for the cannery. Castle and Cooke again acquired direct ownership of the cannery in a corporate merger with Bumble Bee Seafoods in 1961 and continued operations until 1984.
3. The four owners of WRAF Corporation are Rex Y. Matsuno (Suisan Co., Ltd., of Hilo, Hawaii), two principals of the United Fishing Agency, Ltd., of Honolulu, and William R. Zappas, a shopping center developer from California.
4. Historical prices would be maintained at about 1,045 tonnes per year sold to the fresh market and 1,550 tonnes allocated to an alternative market. A fleet of 17 vessels of the current average size would sustain both a one-line cannery and the fresh skipjack market using only local production.
5. Boggs and Pooley (1987) review current problems in the skipjack industry with respect to both biology and economics.

6. As many as 15 percent of the Hawaii population engage in the small-boat recreational fishery. Most of the recreational catch sold goes directly to small stores and outlets rather than to established markets and so is not accounted for in official surveys or records.
7. Hawaii Division of Aquatic Resources (HDAR) data on commercial landings have been hampered by incomplete reporting of some large tuna vessels and by the lack of a reporting requirement for the recreational category.
8. In the Hawaii case several species are marketed on the U.S. mainland, which is analogous to an external market linkage.
9. The actual skipjack fleet without cannery sales will most likely be four to five vessels. The outcome depends on the skipjack fleet's competitive position relative to other tuna fleets in the domestic fresh market (Hudgins 1987).

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Introduction: Limited Access, What is it and why?

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Despite its wide acceptance in other fisheries, limited access remains a controversial topic among Pacific coast groundfish fishermen and fishery managers. It is controversial because it immediately opens a wide array of public policy issues. How should the public conserve fish stocks, and who should benefit from harvesting those fish? What are the costs and benefits to the public, the taxpayer, the fishing industry, and the coastal communities supporting the groundfish industry? Should the government push the industry to be economically efficient in harvesting; or should it discourage technical efficiency to conserve fish stocks? Should management preserve the economic status quo by protecting existing harvest shares? These are the broad issues occupying the discussions of policy makers and academic writers concerned with resource management.

The goal of this introductory section is to define limited access, to dispel some basic misunderstandings about limited access, to clarify the optional forms of limited access, and to review the various resource management objectives addressed. This should set the stage for the following more lengthy discussions. By reducing the scope of needless misunderstandings, it should also help to make future discussions of limited access more productive.

WHAT IS LIMITED ACCESS?

Limiting access in commercial fisheries is commonly implemented through either license limitation programs or assignment of quantitative harvest rights. License limitation, most commonly known as "limited entry," is the simplest and most widely used form of limited access in the United States. A license limitation system issues permits to specific individuals (usually fishermen or fishing vessel owners) and prohibits landings by those not having a license. As will be explained at length in later chapters of this report, licenses can be annually renewable or perpetual fishing rights; they may be openly tradeable or strictly assigned to a particular person; they may be specific to a gear type or species of fish. A wide range of conditions and limitations can be placed upon the exercise of the fishing rights bestowed through issuance of a license.

Rather than simply identifying who can fish, quantitative harvest rights designate how much each license-holder can take. Like license limitation, a quantitative harvest rights system can take on a number of different characteristics. A variety of terms have been coined for the various quantitative harvest rights schemes. These include (1) individual fisherman quotas based upon Francis Christy's original proposal in 1973, (2) individual tradeable quotas as recently adopted in New Zealand (Clark and Duncan 1986), (3) quota licenses as proposed by Canada's Commission on Pacific Fisheries Policy (Pearse 1982), and (4) quota shares or allocated vessel quotas (Clark 1980) which represent individual shares of total allowable catch. Throughout most of the discussion we will use the term "individual fisherman quota" (IFQ), recognizing that individual quotas may be allocated to vessel owners or fishing enterprises rather than to fishermen per se. Regardless of what term is used, a quantitative harvest rights system controls the total harvest by distributing harvest shares among participants in the fishery.

To some degree all fishery regulations dictate the conditions under which fishermen are allowed access to fish stocks. Traditional forms of fishery regulations—including harvest quotas with season closures, gear requirements, size limits, and trip limits—restrict access to fish stocks. This is an inherent part of defining terms and conditions for legal resource use. To control annual harvests, these regulations must reduce the level of fishing effort from what it would be without regulation. Hence, all fishery conservation regulations, both traditional fishery regulations and limited access, conserve fish stocks by controlling the level of fishing effort, and this requires placing limits on use of the stock.

What then is the essential difference between a limited access system and the traditional approach to fishery regulation? The main difference is that traditional regulations seek directly to control harvest levels without saying who should be allowed to take a portion of the total allowable harvest; limited access systems begin by identifying who is permitted to harvest and, optionally, how much they are allowed to harvest. Traditional regulations control aggregate fishing mortality; limited access establishes limits to individual fishing rights.

Limited access will not necessarily supplant all traditional regulations. License limitation, for example, does not directly control the level of harvest by license-holders. Consequently, it may need to be supplemented by fishery-wide quotas and technical restrictions on vessels and gear. Similarly, even though an individual quota system inherently controls total harvest, additional regulations may be needed to achieve optimal utilization of the fish stocks. This is especially true in multi-species, multi-gear fisheries where it is desirable to control size-at-capture, incidental catches, and discards.

Limited access is commonly practiced without government regulation. Common law gives property owners exclusive (but limited) rights to use, to prevent others from using, and to sell property. There are cases of limited access without legal sanction, such as in the famous Maine "lobster fiefs" (Acheson 1975) in which fishing rights to local areas were recognized based upon historic or cultural tradition. Private rights to land, forests, and other forms of property imply limited access and use. The point is that access to the resource for harvesting purposes is limited to some identifiable set of people. Where legally defined rights exist, the owners of these rights may sell, trade and bequeath the rights to others. Because rights can be sold, the identity of resource owners and users may change over time. Access to the resource is limited to those who possess use rights; but the right to acquire ownership is open to all those who wish to obtain use rights by paying the market price or complying with state-imposed qualifications.

All property rights are circumscribed by the law. An owner of urban land must comply with zoning laws. An owner of cattle can continue to feed the animals or slaughter them for market, but he/she must obey law concerning cruel treatment of animals. Ownership in a limited access system permits harvest under specific conditions, but does not permit liquidation of the fish stock. The fish stock in the ocean remains public property managed by the state as a public trust. When licenses and IFQs are marketable, they take on many characteristics of property, including a market price. Nevertheless, fishing rights are use rights, and these are not the same as property rights in the fish stock itself.

WHY CONSIDER LIMITED ACCESS? WHAT'S DIFFERENT ABOUT FISHING?

Commercial fishing differs from farming, small-scale retailing, and other competitive American industries in many respects; the most important is the lack of private property rights in an essential resource. Unlike farmland and mineral deposits, marine fish populations cannot be owned by the users. Historically, in western Europe and North America, property rights to marine fish stocks did not evolve in parallel with rights to land-based resources. Two principal reasons for this are apparent. First, it was not until the rapid expansion in world fishing after World War II that conservation of marine fish stocks was recognized as a serious and widespread problem. So long as people believed in the inexhaustibility of marine fish, there was no widespread desire to develop institutions for limiting access to fisheries. Second, creation and enforcement of rights to marine fish are difficult tasks. Fish are not easily observed and fenced like a plot of land. To establish, enforce, and exchange property rights to fish requires special institutions, legal mechanisms, and ways of doing business.

Today, Pacific coast groundfish stocks are open access or common property resources. With open access resources, there are no restrictions on who can harvest or upon individual harvest levels. An open access resource is literally no one's property (not strictly property at all). In contrast, a common property resource is owned by members of a group or community. Owners have equal use rights. From the standpoint of licensed commercial fishermen, a license limitation system converts a free access resource into a common property resource. Although the licensed fishermen are not legal owners, they become a closed group of resource users, like the animal grazers using a common pasture. With either open access or common property, competitive free enterprise among resource users cannot be expected to assure adequate resource conservation. Additional restrictions on harvests are needed. This need has long been recognized, and it is the reason for public fisheries management.

Harvesters of an open access or common property resource often fail to take appropriate conservation action. It may not be readily apparent to an individual that his use affects the resource size and, ultimately, the profits of all resource users. When there are a myriad of others fishing, a single fisherman will have difficulty even detecting the effect that his own catch has on the overall abundance of fish. Even when fishermen are aware that they affect the size of fish populations, they may take no conservation measures unless they are assured that other users will act in concert to achieve the future benefits of conservation. New entrants may dilute the benefits of conservation when economic returns show improvement.

Thus individual actions, based upon self-interest, cannot assure adequate conservation and cannot effectively promote long-term economic returns from common property or open-access natural resources. Collectively, however, resource users can gain through appropriate restrictions on use. This is true of groundwater basins and public grazing lands as well as fish stocks. Restrictions on individual resource use can be effected through cooperative agreements among users, through certain regional resource agencies like water districts, or even through Federal regulations. In all cases, optimum management requires that individual incentives for short-term economic gain be brought into line with sustainable levels of use.

Regulation of water and grazing lands normally involves quantitative limits to individual use. In medieval England many villages had commons which were regulated through "stinting," a term for limiting the number of animals grazed by individual peasants. These rules for common property use continue in modified form to modern times. Similarly, sheep and cattle ranchers using public grazing lands in the western United States are allocated so many "animal unit months" (AUMs) which roughly corresponds to a known quantity of forage harvested. Farmers irrigating fields in central California each have a quantity of water to which they are entitled. This entitlement may be attached to the land as a water right. These water and grazing rights are forms of limited access in that they designate both (1) which individuals have use rights and (2) the amount of use allowed.

These forms of limited access are not intended to prevent people from becoming farmers or cattlemen. There is no list of licensed or "qualified" farmers. If you want to try your hand at raising almonds in Kern county, California, you can buy or rent land and obtain the necessary water rights. There is free entry to the industry. Fishing, farming, and retailing are similar in this important respect. To exercise this right of free entry, a business firm must acquire the necessary implements and materials. In farming or ranching one requirement is a source of water or rangeland forage. In an open access fishery, however, a new entrant cannot acquire rights to a given quantity of fish. A newcomer simply dips into the common pool, often taking a portion of the available harvest away from established fishermen.

Rather than establish a limited number of quantitative use rights, groundfish managers have established aggregate harvest quotas (or guidelines) and have instituted other restrictive rules on fishing enterprises in order to achieve economic and social objectives. Individual fishing firms then compete for fish based upon harvesting capacity and skill. When quotas are inappropriate, managers may prefer to restrict effectiveness of the gear (such as maximum allowable length of gill nets) or the portion of the stock that is vulnerable to harvest (mesh size regulations, for example). Pacific coast groundfish regulations incorporate many of these methods. While these harvest regulations may adequately prevent fish stock depletion, they do not address a number of other problems.

Economic and social problems frequently occur in quota-regulated open access fisheries. Some of these problems are:

(1) Economic profits are lost to increased fishing costs. Because individual fishermen can maintain or expand their individual harvest shares only by catching fish at a faster rate, they tend to compete by increasing fishing capacity. This is costly for the individual vessel owner, but may result in increased earnings for the vessel. When the fish stocks are under quotas, increased fishing capacity results in no increased fish catch but does raise the total cost of taking the quota.

(2) Overcrowding and gear conflicts occur. Fishermen concentrate in the best fishing areas and during the best fishing seasons. In some cases this results in a very short and furious fishing season which may pressure individual fishermen to operate under unsafe conditions. This can cause loss of gear and can increase the cost and risk in operating a fishing vessel.

(3) Economic instability due to changing profits and harvest regulations. Excessive numbers of new entrants are often attracted to fisheries during periods of higher-than-normal profits. Many of these new firms will go bankrupt under normal circumstances, leaving the fishing fleet overbuilt and with many small firms in financial trouble. While cyclical instability affects many industries, its impacts are amplified in quota-regulated commercial fisheries. This instability is often further amplified by changing harvest regulations. When new vessels swarm into a fishery during good years, managers will tighten the harvest regulations in response. Unstable regulations make it more difficult for established fishing vessel owners to plan for the longer term.

(4) With large amounts of redundant harvesting capacity, regulatory burdens and management costs become excessive. To assure adequate fish stock conservation, there must be restrictive fishing regulations. Annual quotas may be augmented by trip limits and other restrictions. To implement regulations there must be many committees, hearings, and enforcement agents. The resulting regulatory bureaucracy is costly.

Limited access to commercial fisheries is in part a response to these social and economic issues, but it may be used also as a resource conservation tool in heavily exploited fisheries. Some Australian license limitation programs, for example, were adopted early enough in the developing fishery to prevent extensive over-expansion of fishing capacity. This provides a substantial measure of protection to the fish stocks. A similar degree of conservation could be achieved in heavily exploited fisheries by license limitation followed by fleet reduction, or by IFQs.

OTHER UNCONVENTIONAL APPROACHES TO RESOURCE CONSERVATION

It should be noted that license limitation and IFQs are not the only alternative approaches to common property resource management currently under serious discussion. A radically different approach would be to levy taxes or royalties on fish landings. This sort of approach has been given serious consideration in designing programs to reduce air and water pollution (e.g., the so-called "pollution taxes"), and public interest groups have pushed proposals to increase charges for irrigation water and for use of public grazing lands where those resources appear to be overused or misused. The basic logic of a tax charge is that it changes economic incentives in the correct direction.

Firms using common property resources and firms relying on publicly subsidized resource development projects, do not bear, nor do they adequately take into consideration, the full cost of resource use. This is related to lack of private property rights. The fishing firm does not have a direct financial interest in the economic value of the fish stock; its only interest is in the portion of the stock that it can capture and sell. Consequently, the cost of reducing the fish stock (i.e., reduced catch rates for all firms and reduced future availability of fish) is not felt directly by the firm and it does not consider that cost in deciding how much to harvest. A rancher, on the other hand, must account for the effects of a reduced herd on the book value of his livestock. Similarly, a hypothetical private fish stock owner would bear the cost of a deterioration in his fish stock. The prospect of reduced asset values associated with overfishing would act as a strong incentive to harvest at an economically efficient level. Since firms fishing on a common property stock do not experience the reduced asset value, they do not have the proper incentives to conserve. One solution is for a public agency to compute what that asset deterioration cost should be and establish a royalty fee equal to that cost. After that, the private firms will have the proper disincentives to overfish.

This proposal has been described in textbooks and academic papers, but has never been applied to a fishery. Some reasons for this are apparent. First, fishery managers are most frequently trained in scientific disciplines that do not explore taxation as a means of regulating behavior. Thus the royalty scheme is generally proposed by an "outsider" and is given less serious consideration than other direct forms of regulation. Second, the political machinery is strongly geared to protecting the rights and financial interests of current resource users. Since the harvest royalty would, at least superficially and in the short run, reduce the income in fishing, it would work to the disadvantage of exactly those resource users who are most clearly represented in the political process. Even though various provisions could be developed to reduce the short-run burden on fishermen and to assure that revenues raised by the royalty were used for resource protection and enhancement, this political aspect raises strong objections to using royalties as a resource management tool.

Other practical reasons for not using landings taxes to manage fish stocks are (1) the computational task is extremely formidable, and (2) the necessary flexibility in tax rate may be difficult to attain in a legislative system. Because the royalty or tax should equal the cost associated with reduced asset value of the fish stock, the tax would have to be adjusted as fish prices, fishing costs, and fish stock abundances change. Given the imprecision in fish stock assessments and the frequency of changes in prices, it is unlikely that the tax rates could be accurately computed and adjusted. Whether the imprecision in tax rates would create more difficulties than, say, imprecision in harvest quotas is a topic for future research and discussion.

Also, authority to set tax and royalty rates is not now delegated to state fish and game agencies or to the Pacific Fishery Management Council. Thus the legislatures would have to change tax rates in a timely and appropriate fashion, or they would have to delegate such power to managing agencies or commissions. It might be possible to develop legislation that would allow agencies to vary royalty rates based upon economic and biological criteria. Because this sort of system has had little political support, it has not been thoroughly examined. Further work may reveal promising alternatives for tax or royalty management, but this will require longer term research and development than license and IFQ options.

OBJECTIVES OF LIMITED ACCESS

Limiting access to commercial fisheries can address a great number of different objectives. Some of the more prominent objectives are as follows:

1. Promote economic efficiency in harvesting.
2. Establish stable and secure tenure to the fishery for licensed fishermen.
3. Enhance the value of fishery products delivered to consumers.
4. Increase and stabilize the profitability of the fishing fleet.
5. Reduce the burden of management regulations on the industry.
6. Reduce the cost of fisheries management born by the public.
7. Secure an equitable distribution of benefits from the fishery.
8. Protect various segments of the fishing industry from other fishermen and non-commercial interests.
9. Help restrain fishing effort and conserve fish stocks.

This list does not include every conceivable objective, but it does illustrate the broad range of considerations that can be addressed. A brief explanation of these objectives will help to focus the discussion.

Economic efficiency in harvesting involves delivering the available raw fish to dockside with the least possible cost expended on fishing, and delivering the fish in appropriate condition and on a time schedule suitable for marketing. Because open access fisheries normally exhibit substantial excess fishing capacity, which is controlled by quotas and other economically inefficient regulations, substantial advances may be made toward this goal through limited access. To actually calculate an efficient harvest program is a difficult task that is rarely attempted. It was recently estimated that an efficiently operated Pacific coast groundfish fishery could generate between $7 million and $17 million annually in net economic benefits. This could be accomplished with a fishing fleet approximately 40% smaller than the fleet operated in 1984. Where the total falls in this range depends mainly on the size of the Pacific whiting fishery. (See Chapter 5 for details.) A new limited access system may not be able to achieve the estimated level of economic gains, at least not without a moderately long adjustment period, but the potential gains are sufficient to make increased economic efficiency an important objective.

Secure tenure in the fishery has at least two dimensions. It means that a fisherman does not have to perform up to a particular state-imposed standard in order to continue in the fishery, and it means that a fisherman is assured of future benefits from sacrifices made to conserve fish stocks. In open access fisheries, and in some license limited fisheries, a fisherman cannot reduce his fishing or stop fishing temporarily in hopes of harvesting larger or more numerous fish later. With secure, individual fishing rights, however, a fisherman can afford to fish more slowly and to wait until fish are of optimal size or in optimum condition.

The quality of fish delivered to market may be improved under a limited access system. Fishermen and processors operating under open access are sometimes forced to compete for fish by harvesting in a hurry. This may result in increased occurrence of spoiled or unnecessarily frozen fish products. This is especially a problem when traditional quota management results in short fishing seasons that overwhelm the processing and distribution sectors. If fishermen are given individual quotas, they are free to stretch out the fishing over a longer period of time. Recent Pacific halibut experience provides the classic example of open-access fishing causing so short and furious a fishing season that costs of processing and storing the high-valued product are higher than necessary, and almost all the fish have to be frozen.

Profits are usually highest when fishing fleets begin exploiting a new fish stock or have a particularly large year-class of traditional fish stocks. The usual tendency, however, is for profits to fall as additional vessels are attracted. If the fleet size grows as the fish stock is depleted, then a period of serious economic dislocation may ensue. Recent experience with rockfish stocks off the Pacific coast provides a case study in this process. A properly managed limited access system would be able to prevent the instability in profits by attenuating the growth and decline in the fishing fleet. Higher fleet profits can be earned when the numbers of fishing vessels are just sufficient to harvest the available yield. Sustained high profits require stability in market prices, costs, and fish stocks. Limited access cannot provide stability in all these, but it does remove one common source of economic instability and should result in higher average annual profits.

Reducing the burden of fishing regulations on the industry is an appropriate goal, but it is unclear what particular change in regulations constitutes a reduced burden. Regulations on gear quantity or design, commercial fishing seasons, and "trip limits" may be viewed as a burden. From an economics perspective, all these forms of regulation cause private fishing operators to incur additional costs. By establishing a reduced and more efficient fishing fleet, limited access may permit some of the regulations to be removed. Whether such a change would result in an overall reduction in burden of regulations is largely a matter of definition and perception.

Reducing the public expenditures on management would relieve the taxpayer's burden of fishery regulations. The current groundfish management system uses public resources to perform necessary biological research and fish stock assessments, to monitor fish landings, to support Coast Guard and State marine enforcement operations, to carry out legal sanctions against violators of regulations, and to make public decisions on management plans. A recent rough estimate of costs associated with Pacific coast groundfish indicates that about $5.5 million is spent on resource assessment, and $5.6 million on management, enforcement, coordination, and communications. (See Chapter 6 for details.) Costs of managing a fishery will, of course, depend partly upon the character of the fishery and partly upon the types of regulations promulgated. If limited access is conducive to lower management costs, this should be an important consideration.

Everyone agrees that fishing regulations should entail an "equitable" distribution of benefits. Although there is no widely recognized definition of equity, there are clear patterns in management practice. In a recent study of twelve government programs that allocate property rights, Rolph (1983) found that policymakers deal with the equity issue by designing regulations to minimize any redistribution of wealth. Where established resource users enjoy benefits of a communal resource (such as in land development, air pollution, groundwater pumping) "the judicial, the legislative, and the executive branches have uniformly supported the claims of historic users when allocating rights." This principle seems to be honored as well by the existing fishery limited-access system. A reasonable way of dealing with the equity question, therefore, may be to assure that no established fishermen suffer a measurable loss due to the access regulations. As a first approximation this can be accomplished by retaining historic allocations of catch among existing gear types, vessel size classes, and geographic subdivisions. Where rapid changes have been occurring in the fishery, it is not clear that historic shares preserve the economic status quo. New entrants and previous operators with new vessels may pose a problem, for example. Nevertheless, initial preservation of historic catch shares under a limited access system provides a simple and operational means of dealing with the equity effect of the new system.

To protect various segments of the fishery from one another may be more than just another form of the equity issue. Where recreational or environmental interests collide with commercial fishing interests, a limit to commercial fleet size may help to quell strong political and economic forces that could eliminate the fishery entirely. California has adopted license limitation programs in the drift gill net swordfish and shark fishery and in the northern California set gill and trammel net fishery in order to deal with politically potent rivalries between user groups. Limited access has proved to be a useful tool for staking out territories and limiting the range of conflict.

Finally, limited entry can assist in conserving fish stocks. In the case of license limitation, the control over fishing effort may be too weak and ineffectual to assure fish stock conservation. On the other hand, an individual quota system provides direct controls over total harvests and may be a useful substitute for other forms of effort regulation.

No single system of regulation could address all nine of these objectives simultaneously and with equal success. A limited access system must be tailored to the specific objectives sought. And it must address the various private and public interests reflected in the objectives discussed here.

CONCLUSIONS

Several conclusions from the preceding discussion are worth repeating and summarizing. First, a limited access system is basically a social mechanism for reducing the excessive competition for fish that occurs when fish stocks are open to all comers. It is an alternative or a complement to traditional quota, season, and gear regulations. Among the alternative regulatory systems, it is uniquely able to address economic efficiency of the commercial fishing industry. In fisheries that are already highly regulated like Pacific groundfish, limited entry should be viewed as one component of a multidimensional management strategy. The choice is not between limiting access to the fishery or having a free and open commercial fishery. Rather it is between one set of regulations on competitive fishing and another set.

Second, there are several varieties of limited access. The two alternatives receiving the most attention are license limitation and IFQs. With either major type of limited access there are numerous variations in detailed application. Much public discussion and participation should be devoted to determining exactly what features to include in a limited access program for any particular fishery. The ultimate allocation of benefits from the fishery would depend upon the detailed decisions made in designing an actual limited access program.

Third, the problems of economic competition for common property or open access resources are not unique to fisheries; adoption of limited access rules are implicit in many other economic systems, including that of private property resource ownership. Rules for use of rangeland, groundwater supplies, and the air have similar features to fishery regulations. While the elusive marine fish populations are not susceptible to subdivision into pieces of private property, the limited access approach attempts to generate some of the conservation and economic benefits that flow from a free enterprise, private property system.

Finally, it is clear that selection of management method determines what fishing rights or privileges, with corresponding economic benefits, are enjoyed by commercial users of the fishery resource. When a season closure or a license limitation is adopted by the fishery management authorities, the fisherman's economic gain from fishing is altered. Thus the nature of fishing rights or privileges is subject to change at the discretion of fishery councils. Commercial fishing rights are not "inalienable rights" like the right to free speech. They are even less secure from political meddling than standard property rights applying to one's personal possessions. To the extent that a limited access system does establish broader and more secure fishing rights, it will place the fisherman in a position much closer to that of a property owner. But the key decisions will remain those of the public managers whose trust responsibility is established by the various state and federal laws.

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Profile of the Groundfish Fishery

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The groundfish fishery off California, Oregon, and Washington is a highly diverse fishery. Several different commercial vessel and gear types harvest a large number of species in all sections of the coast. Recreational hook-and-line fishing is important as well, especially in central and southern California. Figure 1 illustrates the International North Pacific Fishery Commission (INPFC) areas for which commercial fishing data and management regulations are reported.

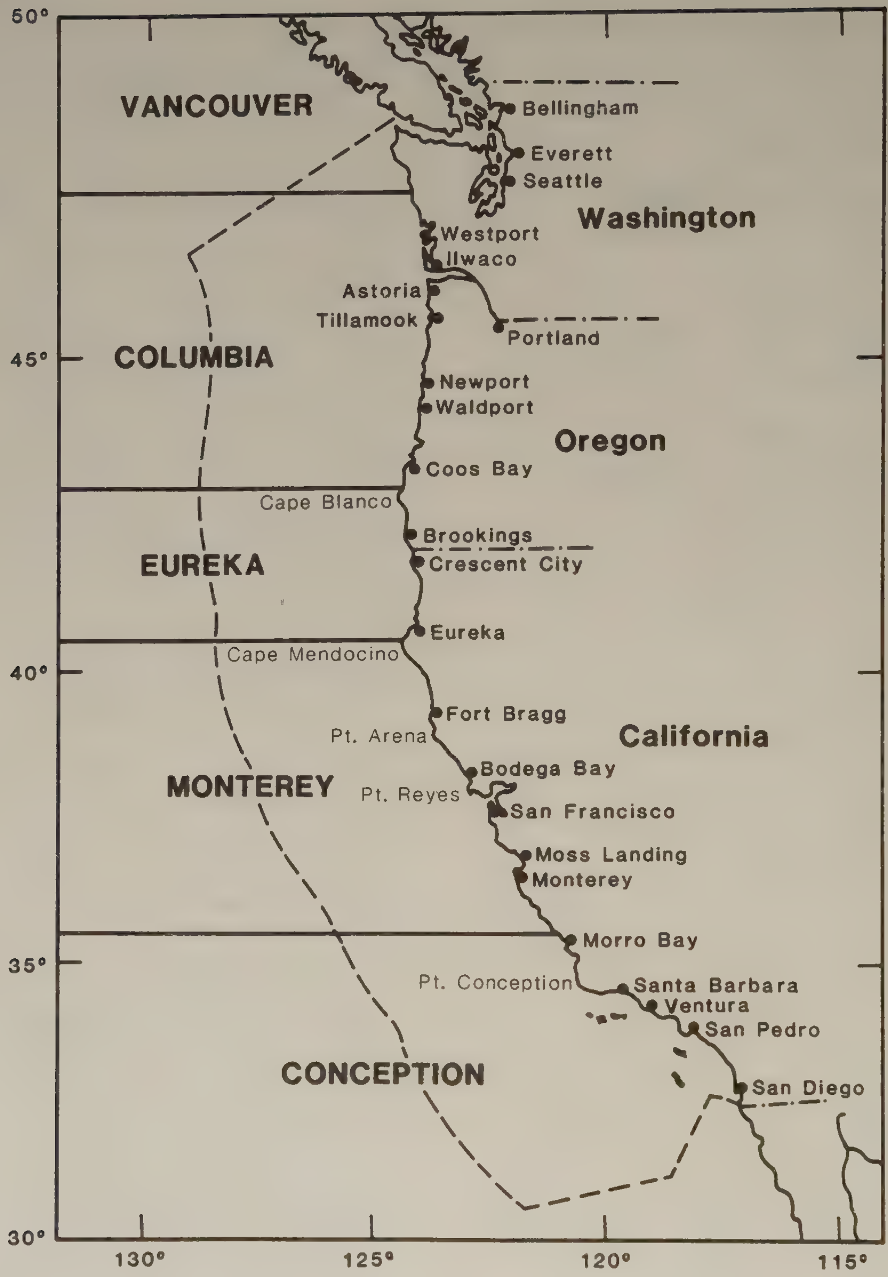
Species classified as "groundfish" include flatfishes (e.g., Dover, English, petrale, rock, and rex sole), roundfishes (e.g., sablefish, Pacific cod, ling cod, and Pacific whiting), a large number of the *Sebastes* species (yellowtail, canary, widow, boccacio, chilipepper, and shortbelly rockfish), and thornyheads (*Sebastolobus*). The Pacific Coast Groundfish Fishery Management Plan also includes certain sharks, skates, ratfish, rattails, jack mackerel, and other fish that are of minor importance to the fishery.

Commercial groundfish fishing is divided into three distinct segments: shoreside domestic landings, "joint venture" harvest, and foreign catch. The quantity and exvessel value of shoreside landings (Table 1) grew from about 60 thousand metric tons (mt) and \$20 million in 1976, to 120 thousand mt and \$60 million in 1982. As the rockfish harvest declined, however, the totals fell to about 90 thousand mt and \$49 million in 1984, although the exvessel value recovered to \$57 million in 1985. As shown in Table 2, most of the commercial stocks of groundfish have been harvested at or near the maximum sustainable levels estimated by the Groundfish Management Team. Unless the domestic fishery expands its harvest of less utilized fish stocks (such as shortbelly rockfish and Pacific whiting), the total harvest is unlikely to grow by more than a few thousand tons.

Since 1978, "joint venture" agreements between domestic trawl fishermen and foreign floating processors have become an important factor in the harvest of Pacific whiting. This provides a major source of income for many of the new, midwater trawl vessels. Annual harvests in joint venture fishing grew to 79 thousand mt in 1984, but fell back to 31 thousand mt in 1985. Since this is still far below the estimated sustainable yield of 175,000 mt, expansion of both joint venture and shoreside landings is possible.

Foreign harvests declined substantially after 1976. With the expulsion of Soviet and Polish trawlers after Soviet invasion of Afghanistan, foreign harvest stopped entirely. In 1985 Polish vessels were again permitted to harvest Pacific whiting. Foreign harvest of underutilized species can continue under Governing International Fishery Agreements negotiated with the State Department until the U.S. fishing industry demonstrates a capacity and intent to take the entire available biological yield.

Tables 3a and 3b show the breakdown of harvests of the most important species groups in 1985 by geographic areas and gear types. Rockfish seem to concentrate mainly in the Columbia area and the Monterey area, while sablefish catch is more evenly distributed along the coast. The Columbia area is most important and the Conception area is least significant for all main species groups. The huge volumes of Pacific whiting caught in Vancouver and Columbia areas are due to the joint venture fishery. From Table 3b it is clear that trawl fishing dominates to an overwhelming degree the commercial harvest of groundfish. Fixed gear (pots and traps, gill nets, and hook-and-line) took a substantial portion of the sablefish in 1985 and a moderate amount of rockfish and other groundfish. The division of catch among the gear types will exhibit some variation over the years, but trawl gear always dominates.


50°
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Oregon
California
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Seattle
Westport
Ilwaco
Astoria
Tillamook
Portland
Newport
Waldport
Coos Bay
Cape Blanco
Brookings
Crescent City
Eureka
Cape Mendocino
Fort Bragg
Pt. Arena
Bodega Bay
Pt. Reyes
San Francisco
Moss Landing
Monterey
Morro Bay
Pt. Conception
Santa Barbara
Ventura
San Pedro
San Diego

Figure 1—Pacific coast region with INPFC statistical areas, major fishing ports, and exclusive economic zones.

Table 1—Pacific coast groundfish harvest quantity and exvessel values. n.d. = no data.

	Domestic harvests					
	Shoreside		Joint venture		Foreign[1]	
Year	1,000 mt	$mil.	1,000 mt	$mil.	1,000 mt	$mil.
1976	57.0	19.4	—	—	255 0	n.d
1977	59.8	20.7	—	—	118.0	n d
1978	71.6	34.5	0.9	0.1	98.0	13.3
1979	90.0	47.9	8.8	1.2	117 0	15 9
1980	87.9	37.1	26.8	3.3	44 6	5 5
1981	103.9	46.8	43.8	6.3	70 9	10 2
1982	119.0	60.0	67.7	10.4	7.3	1.1
1983	97.7	52.2	72.1	10.2	—	—
1984	89.6	49.1	79.0	11.8	14 8	2.2
1985	89.8	57.0	31.6	3.8	50.2	6 1

[1] Foreign fishery value calculated on assumption that price is equal to joint venture average price per metric ton.

Sources: Pacific Fishery Management Council (1982, 1986).

Table 2—Pacific coast groundfish harvests, estimated maximum sustainable yields (MSY), and allowable biological catch (ABC). n.d. = no data; * = MSY estimated to be at least as large as ABC.

	Annual harvest				
Species	1976	1982	1985	MSY	ABC 1986
Arrowtooth flounder	n d.	n d	2,568	—	—
Dover sole	13,179	20,916	20,525	24,398	27,900
English sole	4,488	2,771	1,871	4,500	1,500
Petrale sole	2,816	2,619	1,826	3,200	3,200
Other flatfish	4,690	11,691	3,455	*	7,700
Boccacio	n.d	n d.	1,250	6,100	6,100
Canary rockfish	n.d.	4,296	2,046	3,500	3,500
Chilipepper	n.d.	n d.	1,001	2,300	2,300
Yellowtail rockfish	n d.	8,715	3,058	3,416	4,855
Pacific Ocean perch	2,336	893	1,375	5,300	1,550
Shortbelly rockfish	—	3	12	44,200	10,000
Widow rockfish	—	25,445	9,026	9,200	9,300
Remaining rockfish	n.d.	n.d.	15,225	*	13,700
Thornyheads	n.d.	n.d.	4,067	4,400	4,400
Ling cod	2,542	3,809	3,809	7,000	7,000
Pacific cod	2,165	910	377	*	3,100
Pacific whiting					
Shoreside	trace	1,023	3,895		
"Joint Venture"	0	67,465	31,512	175,500	300,000
Foreign catch	231,000	7,089	50,563		
Sablefish	7,028	18,592	14,580	7,200	10,000
Other roundfish	5,187	4,918	5,723	*	14,700
Totals	295,482	193,550	170,146	339,414	430,805

Sources: 1976 harvests from Pac. Fish. Manage. Counc. (1982), Table 8.
1982 and 1985 harvests from PACFIN Rep. 001.
MSY estimates and ABCs from Pac. Fish. Manage. Counc. (1985).

Table 3a—1985 Pacific coast commercial domestic harvests (mt) by INPFC area and species group.

Species group	Vancouver	Columbia	Eureka	Monterey	Conception	Total
Rockfish	3,406	14,684	6,024	9,751	2,892	36,800
Sablefish	5,745	5,307	2,480	3,214	269	14,016
Pacific whiting	14	885	2,996	—	—	3,895
Other roundfish	2,253	2,340	(	6,902	)	11,495
Flatfish	4,306	9,262	7,203	7,619	1,847	30,237
Others	123	45	97	113	101	479
Total	14,819	30,424	(	51,679	)	96,922

Source: PACFIN Rep. 001. Includes joint venture catch.

Table 3b—1985 Pacific coast commercial groundfish harvests (mt) by gear type and species group.

Species group	Groundfish trawls	Pots and traps	Shrimp trawl	Gill nets	Hook-and line	Other
Rockfish	29,692	56	372	2,996	1,764	1,915
Sablefish	7,194	3,574	34	231	2,665	343
Pacific whiting	3,886	—	7	1	—	1
Other roundfish	14,300	4	—	416	208	418
Flatfish	30,016	1	54	54	57	57
Others	289	—	1	116	39	34
Total	85,377	3,635	468	3,814	4,733	2,768

Source: PACFIN Rep. 009.

Coinciding with the growth in groundfish harvest was an expansion in commercial fishing fleet size (see Table 4). The greatest increase in fishing capacity is due to additional trawl fishing vessels. The number of active Pacific coast trawlers grew from about 270 in 1976 to 444 in 1982. Recent financial difficulties (which coincided with decreased rockfish harvests and some lower groundfish exvessel prices) have caused the trawl fleet to shrink by about 87 vessels. During the same period of nine years, the number of vessels fishing with fish pots or traps grew from 36 to 207 and then fell back to 34. This pattern of growth and decline was widely attributed to the changing Japanese demand for sablefish, the major target species for fish pots.

Longline (or setline) fishing vessels target mainly on sablefish and rockfish, although they take significant amounts of ling cod as well. Some Pacific halibut is taken by longline off the Pacific coast, but in comparison with the Gulf of Alaska fishery this is a relatively insignificant fishery. The number of hook-and-line fishing vessels has remained in the neighborhood of 200 in recent years.

Set net fishing (including gill nets and trammel nets) for groundfish species has expanded in two areas. In central and southern California (i.e., the Monterey and Conception statistical areas) there were nearly 900 licensed gill net fishermen in 1984. Gill net harvest grew from about 1,460 mt in 1981 to 3,814 mt in 1985. California groundfish set gill and trammel nets catch mainly rockfish, ling cod, California halibut, and croakers. The number of commercial set net fishermen is limited by a State license limitation program. The second area of gill net expansion is the Washington coast, where the success of one experimental gill net fisherman in 1980 has led to the entry of a dozen additional commercial set net operators. Operating at depths ranging down to 200 fathoms in canyons, the

Table 4—Groundfish fleet size, 1976-84.

Year	No. vessels with specified gear Otter trawl[1]	Pot/trap[2]	Longline[2]
1976	269	36	N/A
1977	286	60	N/A
1978	351	119	N/A
1979	472	207	299
1980	458	116	205
1981	408	66	191
1982	444	82	208
1983	436	61	184
1984	398	34	[3]96
1985	357	32	[3]129

Source: Korson and Silverthorne (1985).

[1] Vessel numbers before 1981 include double-counting of vessels fishing in more than one state.

[2] Vessels landing fish with these gear types in two or more states are counted more than once.

[3] These numbers represent only Oregon and Washington with double-counting eliminated. California data not available at time of publication.

set nets catch primarily sablefish, "slope" rockfish, arrowtooth flounder, and spiny dogfish.

Pacific coast groundfish fishermen often take nongroundfish species as well. In 1981, for example, 152 of the 340 coastwide shrimp trawlers switched to groundfish trawl gear for at least part of the year. Due to poor shrimp yields in 1982 through 1984, nearly all of the pink shrimp trawlers converted to groundfish trawling. This is one source of new entrants to the groundfish trawl fleet. Ability to shift among target fisheries is also exhibited by smaller inshore trawlers of the Crescent City area which fish for Dungeness crab in the winter and trawl for sole and rockfish during the fall and spring.

Groundfish vessels display a significant amount of geographic mobility as well. It is not uncommon for midwater trawl vessels to fish in joint venture operations off the West coast or in Alaska during the spring and summer, but to fish rockfish for shoreside processors during the winter. Nearshore, flatfish trawlers are known to make seasonal shifts between ports as distant as Crescent City and Morro Bay, California. Similarly, large groundfish processors are not reluctant to purchase raw fish from geographically dispersed sources. A Eureka area processor, for example, may buy fish in Coos Bay and San Francisco when it is convenient to do so.

Both economic reasoning (see Huppert 1979) and statements by industry members suggest that the degree of flexibility reflected in the geographic, gear, and species switching in the commercial fleet is an important aspect of business strategy. When market prices and species availability exhibit unanticipated fluctuations, commercial operators with experience and expertise in several different fisheries have an advantage. They can respond by shifting among fishing activities which will reduce their business risk by "diversification," in much the same way that investors diversify among stocks, bonds, and other assets. Many trawl fishermen consider it essential that management regulations allow them to move between joint venture fisheries (either Pacific coast or Alaska) and shoreside domestic fishing, between bottom trawling and midwater trawling, and between shrimp and bottom trawling. This multipurpose capability must be recognized in designing a limited access system.

Table 5—Catch and revenue share distributions among 401 active groundfish trawl vessels, 1983 and 1984.

Top % of vessels	% of groundfish catch 1983	 1984	% of revenue 1983	 1984
10	35.6	32.9	32.6	30.4
20	57.0	53.7	53.3	50.8
30	71.6	69.1	67.6	65.7
40	82.0	80.8	78.5	77.4
50	89.1	88.5	86.4	85.8
60	93.9	93.8	92.1	92.0
70	96.9	97.0	95.9	95.9
80	98.9	98.9	98.5	98.4
90	99.8	99.8	99.7	99.7

Source: Annual summary records for vessels using bottom, groundfish, or midwater trawl gear. Includes domestic landings and exvessel revenue from all species landed by trawl vessels.

Table 6—Technical changes affecting fishing power and safety characteristics of Pacific coast trawlers.

Technical innovation	% adopting Before 1980	 1980-84	 Total
Midwater trawling	3.7	18.1	21.7
Chromoscope	1.2	43.4	44.6
Sonar	21.7	19.3	41.0
Track plotter	13.3	48.1	61.4
Radio facsimile	3.6	7.2	10.8
Survival suit	48.2	32.5	80.7
EPIRB	8.4	16.9	25.3
Personal computer	4.8	6.0	10.8

Source: Dewees (1985).

Another fleet characteristic important to the operation of a limited entry system, the concentration of harvests among a small proportion of vessels, is displayed in Table 5. To construct this table we ranked domestic trawl vessels in order of annual tonnage landed and exvessel value of shoreside landings in 1981 and 1982 (not including joint venture catch). The top 10% of the fleet caught 43% of total fleet landings in 1981 and 44% in 1982. Ninety percent of the total catch was taken by only 50% of the nominal trawl fleet. Exvessel value of landings is not quite so concentrated in the upper end of the fleet, indicating that higher volume of landings is associated with lower value per ton landed. We expect that concentration of volume and value of landings would be about the same in recent years.

The technical capabilities of commercial fishing vessels are being steadily improved. Dewees (1985) has recently studied the rate of adoption of technological innovations by the trawl fleet. Table 6 summarizes some of Dewees' findings based upon interviews with 83 trawl vessel operators during 1984. Of the eight technical innovations examined, the four that seem to contribute most directly to fishing power are midwater trawling, chromoscope, sonar, and track plotter. The radio facsimile, survival suit, emergency position indicator radio beacon (EPIRB), and personal computer are

Table 7—Length distribution (ft) of trawl vessels in 1984, and disposition of 100 vessels missing from the active fleet in 1984.

	<30	30-39	40-49	50-59	60-69	70-79	80-89	>90
1984 fleet	2	20	100	108	105	44	11	8
Known losses	1	5	25	27	26	11	3	2
Sunk	0	1	[illegible]	12	10	6	1	2
Alaska and other	0	0	0	3	5	3	3	4
Repossessed	0	1	4	1	5	5	2	1
Inactive	0	1	2	4	1	0	0	0
Other	0	0	2	4	4	0	1	0

Note: A total of 201 trawlers that landed groundfish on the Pacific coast during 1981-83 did not land fish during 1984. Of these we have information on the disposition of 103. For three of these we do not know the vessel length, and they are not reported in the table.

more closely related to safety and convenience. While the specific contribution of any of these innovations to fish harvest capability or safety would be difficult to quantify, the fact that new equipment is rapidly adopted by a significant portion of the fishing fleet indicates that fishing capacity is changing and expanding in many dimensions. This suggests that it would be a mistake to rely heavily upon the number and size of vessels as a simple measure of fleet capacity.

Due to both the changing technology and the wide variation in landings among vessels, one cannot assume the fleet's harvest will be proportional to number of active vessels. Consequently, a license limitation program coupled with attrition or voluntary "buy-back" of licenses may have surprisingly little effect on fleet capacity. Even if "high-liners" are targeted in the fleet reduction, it is possible for licensed vessels that were previously low producers to become high-liners.

During 1983 and 1984 the trawl fleet was beset by falling rockfish quotas, falling sablefish and Dover sole prices, and a backlog of high interest-rate loans. One result was an unusual number of losses from the fleet due to bankruptcy, bank repossessions, sinkings, and transfers to other fisheries. Of the 599 trawlers known to have made commercial sales of groundfish during 1981-84, a total of 201 were no longer in the Pacific coast fishery in 1985. We were unable to ascertain the fate of all 201 vessels, but information on 100 vessels has been summarized in Table 7. This shows that losses from the fleet occurred among almost all sizes of vessels and that there was no disproportionate loss from large or small size categories. Forty-five percent of the known losses were due to sinkings or burnings, 21% percent were repossessed and inactive, 20% of the vessels were fishing in Alaska, 8% were fishing in other fisheries, and 6% were still afloat but not fishing.

The financial hardships reflected in these losses from the trawl fleet had a variety of causes, and have elicited a variety of suggested solutions, including a return to use of mesh size restrictions rather than species quotas; elimination of trips limits on rockfish; greater involvement of industry representatives in management decisions; grouping of species quotas to reflect catch groupings; leaving regulations unchanged for longer periods of time; prohibition of discards; prohibition of gill nets; better stock assessments by biologists; creation of a separate California regional fishery management council; reduced dependence of management on fishery data (i.e., fish tickets and logbook records); and placement of a moratorium on trawl vessel licenses. All of these suggestions (and many others not listed here) have been delivered in person or in writing to the Pacific Fishery Management Council and its subgroups. Many deserve serious attention by the management agencies. However, financial and management problems prompting the trawl license moratorium proposal and some of the other more controversial proposals seem to have declined since 1984. This may provide a needed respite for careful and thorough consideration of a range of new management alternatives, including license limitation systems and individual fishermen quotas.

CONCLUSIONS

Based on this short review of the groundfish fishery, several important implications for discussion of limited access are evident. First, both the total levels of harvest and the trawl fleet size seem to have peaked in 1982. Future growth of the fishery will depend upon increased exploitation of less valued stocks such as Pacific whiting and shortbelly rockfish. There seems to be more than sufficient fishing capacity for the traditional species. Second, geographical and biological diversity of the fishery resources results in a wide variety of fishing operations. Although trawl vessels dominate the catch, the pot, longline, and set net fleets harvest substantial amounts of fish as well. Third, flexibility in fishing patterns by the predominant trawl fleet suggests that a harvest rights system requiring fishermen to specialize in predetermined areas, species, or gear might be too restrictive for economical fishing operations. Finally, the concentration of harvests in a small portion of the fleet, and the pace of change in fishing technology, indicates that simple controls on fleet size cannot be expected to wield much control over fishing capacity or harvest levels.

Potential Economic Benefits and Optimum Fleet Size in the Pacific Coast Trawl Fleet

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Abstract Limiting entry to the Pacific coast groundfish fishery poses two principal questions: (1) How large are the potential economic returns under limited access management? and (2) Will the economic benefits exceed the program costs plus costs associated with transitory dislocations in the fishery? This paper reports on a partial evaluation of the first question, based on a mixed integer programming model that computes optimum fleet size, fishing effort configuration, and associated economic surplus. The multispecies fishery, economic parameters, annual harvest constraints, and summary results are presented. Overall, a maximum economic profit of about $12 million can be generated by a trawl fleet that is about 38 percent smaller than the baseline 1984 fleet with a 23 percent reduction in weeks fished. Another important conclusion is that economic profits would suffer if fishing vessels are prevented from shifting among groundfish, pink shrimp, and joint venture fisheries.

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Introduction

The principal objective of this paper is to evaluate the magnitude of economic benefits from limiting access to the Pacific coast trawl fishery. An extensive literature describes the conceptual advantages and disadvantages of various approaches to limited access (Christy, 1973; Rettig and Ginter, 1978; Stokes, 1979; Young, 1983; Rettig, 1984). Ideally, a fishing industry under limited access will minimize the cost of catching the sustainable biological yield. This should create a source of surplus economic value which may be collected as rent by public agencies or retained as profit by private industry. As a practical matter, to justify a new limited access regime it needs to be shown that potential economic surplus exceeds the social and economic costs associated with temporary dislocations and continuing program administration. In anticipation of the need for evaluating limited access in Pacific groundfish we evaluate the optimum fleet size and fishing effort patterns for a profit-seeking centralized owner/manager of the fishery. This estimate provides a useful benchmark for program evaluation, and it represents the social opportunity cost of not adopting limited access.

The Pacific coast trawl fishery is represented by a linear production model, which assumes that several varieties of fishing effort are each supplied at fixed unit costs and that the catch for each variety of fishing effort is proportional to the level of effort. A mixed integer programming algorithm is used to compute the maximum economic surplus subject to constraints on the annual harvest of various groundfish species and constraints on the amounts of fishing effort that fishing vessels can exert. Fish prices, fixed and variable fishing costs, and catch rates for each species are determined from data on the fishery. The solution gives optimum numbers of vessels, optimum allocation of fishing effort, and maximum economic value.

Several recent studies have applied linear programming (LP) to multispecies fisheries. Brown et al. (1979), Siegel et al. (1979), and Overholtz (1985) develop LP models of the New England trawl fishery. Each of these uses a harvest production model in which fishing is directed toward target species while "bycatch" of other species is taken in smaller quantities. Although the term "bycatch" may be a useful descriptive device in some fisheries, we find that trawl vessel captains frequently harvest two or more species in combination without considering one species to be a bycatch (i.e., a coincidental or unplanned consequence) of another target species. Without identifying any species to be a target or a bycatch, the Pacific trawl model specifies a joint production technology consisting of several fixed-proportions multispecies fishing modes. The mix of species caught per unit effort varies among vessel sizes, among seasons, and among fishing modes. In contrast to the New England models this model adopts maximum economic surplus, rather than maximum catch or maximum exvessel value of catch, as the objective.

The Pacific Coast Trawl Fishery

Both the trawl fleet and the fish stocks are spread among three major areas of the Exclusive Economic Zone off the Pacific coast (Figure 1). The northernmost area consists of the International North Pacific Fisheries Commission's (INPFC) Columbia area and a portion of the Vancouver area. The middle area is INPFC's Eureka area, which includes the major southern Oregon and northern California ports. The southernmost area, Monterey, covers central California. We have not included the INPFC Conception area because little groundfish trawling occurs there.

A total of fifty-one species are considered in the trawl fleet model. Forty-nine groundfish species are grouped into eight major categories (Table 1). Dover sole, sablefish, widow rockfish, and Pacific whiting are each treated separately due to their importance to the fishery, availability of specific stock assessments, and consistency with management regulations. Eight species are grouped in "other flatfish," the most important of which are English and petrale sole, flounders, and sand dabs. "Other rockfish" includes twenty-four *Sebastes* and *Sebastolobus* species. Pacific cod and ling cod are placed in a separate group, because they are distinct from the flatfish and rockfish species in both biological and economic characteristics. The miscellaneous group includes various sharks, skates, rays, grenadiers,

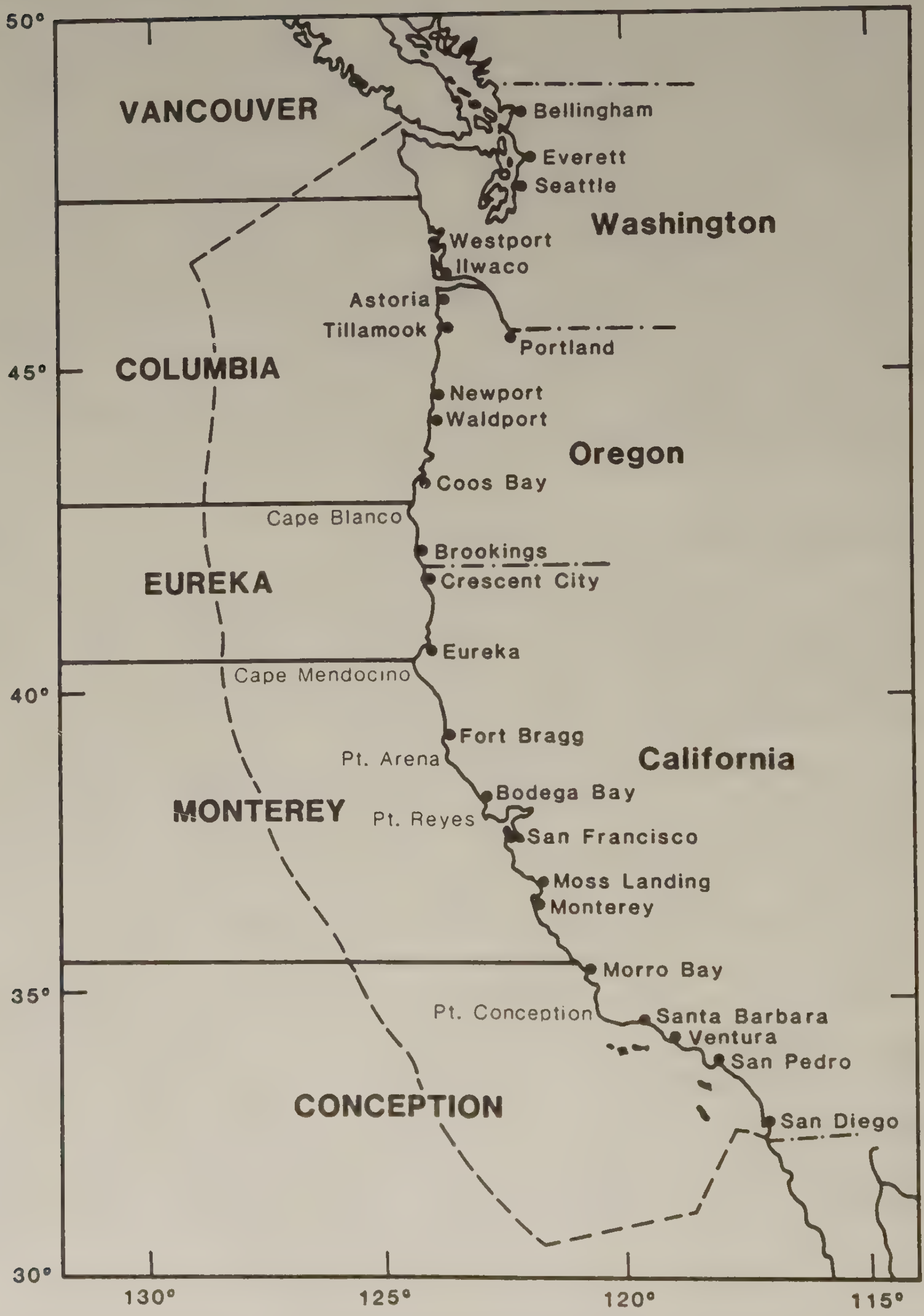
50°
45°
40°
35°
30°
130°
125°
120°
115°
VANCOUVER
COLUMBIA
EUREKA
MONTEREY
CONCEPTION
Washington
Oregon
California
Bellingham
Everett
Seattle
Westport
Ilwaco
Astoria
Tillamook
Portland
Newport
Waldport
Coos Bay
Cape Blanco
Brookings
Crescent City
Eureka
Cape Mendocino
Fort Bragg
Pt. Arena
Bodega Bay
Pt. Reyes
San Francisco
Moss Landing
Monterey
Morro Bay
Pt. Conception
Santa Barbara
Ventura
San Pedro
San Diego

FIGURE 1. Location of Pacific coast fishing ports, landmarks and INPFC statistical areas.

Table 1
Total Allowable Catches for Groundfish Species, and Assumed Catch Constraints for Pink Shrimp and Dungeness Crab.

Species	Sub-Areas Vancouver-Columbia	 Eureka	 Monterey	Total
	shorts tons			
Dover sole	15,318	8,816	5,510	29,644
Other flatfish	6,643	2,877	3,319	12,839
Code & lingcod	7,801	537	1,098	9,436
Widow rockfish	7,270	1,429	1,549	10,248
Other rockfish	13,563	2,965	9,461	25,989
Sablefish	3,502	1,924	1,776	7,207
Pacific whiting	—	—	—	209,380
Miscellaneous	10,113	1,309	1,591	13,013
Pink Shrimp	—	—	—	17,218
Dungeness crab	—	—	—	2,477

arrowtooth flounder, and others. In addition to the groundfish species, two important shellfish—pink shrimp and Dungeness crab—are included as alternatives to finfish.

Pacific coast trawlers display a wide range of sizes and vintages. For convenience we have designated five vessel length classes based upon Coast Guard registered length: (1) 40–49 ft., (2) 50–59 ft., (3) 60–69 ft., (4) 70–79 ft., and (5) 80–95 ft. Vessels in the two smaller classes are generally older, are often wooden-hulled, and make inshore trips of limited duration. Because they are less seaworthy in rough weather, the smaller vessels typically spend less time at sea during the winter. Intermediate-sized and large vessels are generally newer, steel-hulled vessels having greater cruising speed and range. They can more easily make trips of longer duration, are less hampered by rough weather, and can participate in a greater variety of fisheries.

The trawl fishery is both multispecies (harvests more than one species at a time) and multipurpose (participates in more than one discrete fishery). An important alternative for groundfish trawlers is pink shrimp fishing. Shrimping, which requires a special small-meshed trawl net, is seasonally concentrated in the spring and fall, and exhibits marked annual variation due to fluctuations in the shrimp populations. All three Pacific coast states have imposed regulatory restrictions on the shrimp fishery. These include maximum incidental groundfish landings, minimum size or count-per-pound standards, and season closures designed to protect egg-bearing females during November 1–March 31 (Pacific Fishery Management Council, 1981).

Another important alternative for trawlers is the "joint venture" Pacific whiting fishery in which midwater trawlers deliver fish directly to foreign-owned fish processing ships. Finally, some vessels replace their trawl nets with crab pots to participate in the Dungeness crab fishery during the late fall and winter. The amount of crab fishing by trawl vessels is usually not great, and represents a very small portion of the total catch in this highly cyclical fishery. Based upon these categories, six different fishing modes are identified: (1) multispecies groundfish trawling in the Vancouver-Columbia area, (2) multispecies groundfish trawling in the Eureka area, (3) multispecies groundfish trawling in the Monterey area, (4) single-species pink shrimp trawling, (5) single-species Dungeness crab pot harvesting, and (6) single-species joint venture fishing for Pacific whiting. The catch rates vary among these six modes, and for each mode they vary among seasons and vessel-size classes.

Model Specification

The mixed integer programming model maximizes economic surplus subject to constraints on total allowable annual harvest and constraints on vessel-weeks fished. The decision variables are: (1) 5 integer variables N_k for the number of vessels in each of the five size classes ($k = 1, \ldots, 5$) and (2) 120 real variables W_{jks} for the number of weeks fished by vessel size class k allocated to each fishing mode ($j = 1, \ldots, 6$) in each season ($s = 1, \ldots, 4$).

The model is specified as:

$$\text{Maximize } Z = \sum_{k} \left(\sum_{js} \left(\sum_{i} P_{ijs} a_{ijks} - C_k \right) W_{jks} - F_k N_k \right) \quad (1)$$

subject to:

$$\sum_{ks} a_{ijks} Wjks \leq Q_{ij} \text{ for all } i, j \tag{2}$$

$$\sum_{j} W_{jks} - N_k W^*_{ks} \leq 0, \text{ for all } s, k \tag{3}$$

where Z denotes economic surplus, P_{ijs} is the ex-vessel price of species i in mode j in season s, a_{ijks} is tons of species i in mode j harvested per week by a vessel of class k in season s, C_k is variable cost per week for vessels in size class k, F_k is fixed costs per year for vessels in size class k, Q_{ij} is the annual allowable catch for species i in mode j, and W^*_{ks} denotes the maximum number of weeks a vessel in size class k can fish during season s. The first constraint, equation (2), represents the limits on biological productivity, while the second constraint, equation (3), indicates the limits on harvesting activity by trawlers.

The technical coefficients a_{ijks} in the catch constraints reflect the assumed fixed-proportions joint-in-inputs harvesting technology for each groundfish mode. This assumption is fairly strong and possibly unrealistic. Trawl vessel operators undoubtedly do target upon various species by choice of timing, depth, towing speed, and gear configuration. The species mix actually observed in groundfish landings is an average of many different species mixes experienced during our base period. These patterns of landings represent complex economic decisions made jointly by fishermen and processors. As with all such economic decisions we would expect the species mix to change following any shift in expected fish prices, fishing costs, market demands, fish abundance or availability, and fishing regulations. Although we have not developed a model of fisherman/processor decision-making, we can expect some significant changes to affect fishing patterns in the long run. In particular, we anticipate that implementation of a limited access system would cause some systematic changes in fish stocks and relative profitability among vessel sizes. The consequent voluntary changes in targeting would raise profits from the level attainable with the initial pattern of targeting. The economic surplus achievable with centralized management, therefore, would be at least as large as that under the assumption of fixed fishing patterns. We conclude that the fixed coefficients technology will cause our model to underestimate the actual economic surplus available under limited access.

The mixed integer programming approach to optimum harvesting disregards several potentially important nonlinearities in the economic and biological relationships. The underlying bioeconomic model is one of static equilibrium. Thus fish prices do not respond to changes in annual harvests; input prices do not vary with total use; fish stock densities and harvest rates do not depend upon the level of harvest; and harvesting technology is unchanging. These conditions are inconsistent with standard market demand curves, input supply curves, and population dynamics models. Thus the results are strictly applicable only if the fishery is very small relative to both aggregate product demand and input supply, and if the range of total harvests analyzed is too small to significantly alter fish stock abundances. The Pacific coast trawl fishery probably comes close to satisfying the economic smallness criteria, but the annual harvests certainly affect fish abundance.

Our model assumes that the observed catch rates reflected in the technical production coefficients are consistent with the sustainable yield levels embodied in the annual harvest constraints. If the calculated optimum fishery does not exhaust all the biological harvest constraints, we would expect, in actual practice, the fish stocks to grow, the catch rates to increase, and the variable returns to fishing to increase. Because the model ignores this effect on catch rates, the model will understate the potential economic surplus.

Mixed integer programming analysis also ignores the historical pattern of operations in the fishery. In the words of Shephard and Garrod (1980), the linear programming method ''happily makes large changes in the pattern of allocation in pursuit of small advantages.'' Since changes from the status quo may be costly, these small advantages may be insufficient to justify adopting associated management policies that disrupt the fishing fleets. Our analysis is clearly subject to this criticism as well. We address this issue by computing maximum net economic values for a sequence of models in which the fleet is constrained to the base year vessel size distribution. This further constraint should reduce the presumed dislocations in the fishing fleet caused by a rapid shift to the optimum fleet configuration.

Model Implementation

Annual allowable harvests for the groundfish species established by the Pacific Fishery Management Council in 1985, as adjusted to reflect proportion taken by trawl gear during 1981–84, are adopted as overall catch constraints (Table 1). Lacking estimates of sustainable yield for pink shrimp and Dungeness crab, we take 1981–82 average total trawl catch levels as constraints. For pink shrimp the harvest constraint is close to the recent 12-year average pink shrimp harvest. The joint venture whiting fishery is initially constrained to the 1984 catch level. Higher and lower harvest constraints for whiting, shrimp, and crab are adopted to test the sensitivity of the model.

Technical production coefficients and constraints on amounts of fishing effort per vessel are based upon weekly catch records during 1981 and 1982 developed for the Pacific Coast Fisheries Information Network (PACFIN) research data base (Huppert et al., 1984). Technical coefficients for multispecies groundfish in each area and for coastwide pink shrimp and Dungeness crab are computed as average weekly catches by size class and season. Each "week" of fishing represents one calender week in

Table 2
Assumed Maximum Number of Weeks Fished per Vessel by Season and Size Class

Size Class	Winter	Spring	Summer	Fall	All Year
1	6.25	9.0	9.31	6.0	30.5
2	7.64	9.18	9.73	6.6	33.15
3	9.13	10.0	9.21	9.07	37.41
4	10.0	10.0	9.67	10.0	39.67
5	11.0	11.0	11.0	11.0	44.0

Table 3
Average Annual Fixed Costs and Weekly Variable Costs for Pacific Trawl Vessels (1984 dollars)

	Class 1	Class 2	Class 3	Class 4	Class 5
Weekly Variable Cost	$ 2638	3795	5518	5669	13,895
Annual Fixed Cost	45,990	49,639	78,535	83,952	110,550

which at least one commercial landing was recorded. Catch rates for Pacific whiting joint venture fishing were based upon information from private companies and financial reports. The assumed maximum number of weeks fished for vessels represents the average weeks spent fishing by the most active trawlers in each size class (Table 2).

Variable and fixed costs were estimated for each vessel size class using annual financial statements prepared for income tax purposes during 1980 to 1983 and using various other, secondary information sources (Table 3). Variable costs include the costs of fuel, oil, provisions, gear, crew and captain's share, payroll expenses, maintenance and repairs, ice, salt, bait, and miscellaneous. Crew and captain's labor payments are the average *share* earned, but we treat labor costs like a weekly wage. Fixed costs include capital costs (depreciation and opportunity cost of capital), hull and liability insurance, and taxes other than income taxes. Costs were adjusted to 1984-equivalent dollars using the GNP implicit price deflator for each year. Exvessel fish prices by area are averages for 1984 as observed in the PACFIN management data base (Table 4).

Variable costs, catch rates, and exvessel prices determine the net return per fishing week for each fishing mode and season for each vessel class. These net returns, which become the coefficients of the weeks fishing variables in the objective function (Equation 1), may be expressed as:

$$r_{jks} = (\sum_{i} P_{ijs} a_{ijks} - C_k) \tag{4}$$

Table 4
Exvessel Prices of Trawl-caught Fish and Shellfish. Price per ton in 1984 dollars. Source: PACFIN Management Data base

Species	Vancouver-Columbia	Eureka	Monterey	Joint Venture
Dover sole	456.4	483.3	459.5	
Other flatfish	561.2	553.0	552.0	
Cod & lingcod	501.3	536.0	515.2	
Widow rockfish	452.0	428.0	452.0	
Other rockfish	497.2	467.0	450.0	
Sablefish	402.8	377.3	335.0	
Whiting	138.0	126.7	182.5	149.4
Pink shrimp	———	1325.0	———	
Dungeness crab	———	2284.6	———	

As shown in Table 5 there are several negative values for these variable returns. It cannot be optimal to deploy fishing effort to categories yielding a negative variable return. A quick scan of Table 5 reveals among other things that no vessels in Class V should be included in the optimum trawl fleet, and that no class I vessels should enter the joint venture whiting fishery. Thus several conclusions can be drawn directly from examination of the coefficients of the fishing weeks variables.

The fishing week constraints do not prevent pink shrimp fishing during the closed season of November 1–March 31. Because recorded shrimp catch during that period is so low, however, the computed variable return per week from shrimping is negative during the winter quarter (January–March). Thus the programming model will not assign trawl vessels to the shrimp fishery during the prohibited winter period. The time resolution of the model does not allow us to examine periods of less than three months. Consequently, the fall portion of the shrimp fishing closure cannot be addressed directly. It is clear from Table 5, however, that the weekly return from shrimping falls markedly in the fall, making this an unlikely period for substantial fishing activity in the optimal program.

A baseline trawl fleet profit was calculated by inserting in

Table 5
Coefficients for Fishing Weeks in Objective Function of Programming Problem. Each entry equals the gross exvessel revenue minus variable cost per fishing week

	Vessel Size Class				
	I	II	III	IV	V
A. Vancouver-Columbia Area Multispecies Groundfish					
Winter	-91.4	-437.2	893.6	3956.1	-4206.1
Spring	1942.6	775.1	284.8	2923.5	-730.5
Summer	2152.9	3219.0	784.1	2533.3	-3469.8
Fall	551.3	875.9	-849.1	1145.4	-59.5
B. Eureka Area, Multispecies Groundfish					
Winter	209.8	-429.5	-112.1	2310.8	-10633.7
Spring	3903.2	1189.1	-1425.3	3089.8	-6723.4
Summer	2512.8	1248.9	260.6	3313.1	-2827.8
Fall	-652.2	-50.0	-1767.6	-52.4	-11394.8
C. Monterey Area, Multispecies Groundfish					
Winter	874.4	919.2	885.9	1878.8	-6953.0
Spring	783.9	719.8	-419.9	222.5	-9560.3
Summer	1720.1	1131.1	-475.0	1800.0	-7229.6
Fall	928.9	1069.3	-429.4	143.1	-12167.9
D. Pink Shrimp Fishing					
Winter	-1219.8	-2469.2	-3822.4	-1601.5	-13895.0
Spring	1880.2	2631.5	2908.6	4149.0	-4023.7
Summer	1231.4	2326.8	1716.0	2386.8	-11814.6
Fall	886.9	644.0	-443.7	412.5	-10661.9
E. Dungeness Crab Fishing					
Winter	-307.2	-1167.4	-2708.4	-528.8	-13894.9
Spring	-1266.8	-2561.0	-5289.9	-5069.2	-13894.9
Summer	1977.3	1482.7	-1429.0	2898.0	-13894.9
Fall	4033.5	3675.9	1929.3	6644.8	-8548.9
F. Joint Venture Whiting					
Spring	-2637.6	5287.9	6049.5	6993.5	-13894.9
Summer	-2637.6	5287.9	6049.5	6993.5	-13894.9

Table 6

Results of Mixed Integer Programming for the Pacific Trawl Fleet[a]

		Optimum fishery[c]		
	(1) Baseline fleet in 1984[b]	(2) JV takes whiting MSY	(3) 1984 JV harvest	(4) With no JV fishery
Number of vessels				
Class 1	106	0	0	0
Class 2	118	245	180	180
Class 3	138	0	0	0
Class 4	55	93	85	58
Class 5	12	0	0	0
Total number	429	338	265	238
Profit ($million)	−10.25	17.7	11.96	7.61
Proportion from:[d]				
Shrimp fishing	.324	.180	.267	.362
Crab fishing	.038	.081	.109	.143
JV fishing	.306	.475	.263	.000
Groundfish	.332	.264	.360	.495
Total weeks	11,763	11,034	9,041	8,054
Proportion in:				
Shrimp fishing	.218	.320	.380	.440
Crab fishing	.044	.042	.050	.060
JV fishing	.074	.280	.130	.000
Groundfish	.664	.358	.440	.500

[a] The solutions to the mixed integer programs were computed on an IBM-PC compatible computer using LP/MIP83, Version 5.00 copyrighted by Sunset Software, San Marino, California.

[b] The 1984 Baseline is not an optimum. The number and size distribution of vessels represents the 1984 fleet while the distribution of weeks fished represents the 1981–82 average. All prices and costs used in calculating profits are in 1984 dollars.

[c] All these assume the pink shrimp harvest constraint equals average 1981–82 catch (17,218 short tons).

[d] This is the proportion of operating profit (or net revenue) not economic profit. Fixed costs of vessels are not allocated among fisheries in calculating this proportion.

equation (1) the weeks fished in 1982, trawl fleet size in 1984, and the cost, price, and harvest rate parameters adopted for the model. The resulting estimate of economic surplus is $\$-10.25$ million (Table 6). This large negative value reflects a fishing fleet that was significantly overbuilt during the 1977 through 1982 period. Allowable rockfish harvests fell sharply during the latter half of the period due to cropping down of previously unfished populations of widow, yellowtail, and canary rockfish. Pink shrimp harvests also fell from a peak of 42 thousand short tons in 1978 to an average of 17 thousand short tons in 1981–82.

Results

Table 6 displays a summary of results from the mixed integer program. Assuming a 1984 level joint venture fishery, the optimum number of 265 vessels is a 38 percent reduction from the baseline trawl fleet in 1984. Optimum economic surplus is $12 million, an increase of over $22 million per year from the baseline fleet profit. Multispecies groundfish trawling accounts for slightly more than ⅓ of the profit, shrimp fishing and joint venture whiting fishing each account for about one-quarter of the profit, and only one-tenth of the profit is from crab harvesting.

The size distribution of vessels in the optimum fleet differs markedly from the baseline. Absence of the largest and smallest vessel size classes in the optimum is not unexpected. Informal discussions with industry members and financial advisors suggested that the smaller vessels are now outmoded and that the largest class of vessel was too large to survive in the domestic Pacific coast fishery after the decline in rockfish harvests. The surprising absence of midsized, 60–69 ft. trawlers in the optimum fleet evidently occurs because the greater harvest rates achieved by these vessels as compared to 50–59 ft. vessels do not sufficiently counterbalance the proportionately greater increase in harvesting costs. The midsize vessels can be profitable in their own right, as shown in Table 5, when deployed in appropriate modes and seasons. But they are not profitable enough to be included in the optimum fleet.

The level and distribution of weeks fished by fishing mode and vessel size class (aggregated over seasons) also differ between the baseline and optimum fleets. The optimum total level of weeks fished is 9,041, a decline of about 31 percent from the baseline fleet to the optimum. Obviously, this fishing effort is concentrated in the second and fourth vessel classes: 63 percent in Class 2 and 37 percent in Class 4. Several other significant changes in fishing patterns occur in the optimization: the proportion of weeks assigned to pink shrimp trawling increases from 22 percent to 38 percent of the total; groundfishing trawling declines by almost one-third; and joint venture fishing for Pacific whiting almost doubles from 7 percent of the total to 13 percent.

A linear programming algorithm is used to calculate shadow prices for those species whose allowable harvests are binding constraints. These shadow prices represent the marginal value of additional harvestable quantities under the optimum fishery. An additional ton of widow rockfish sustainable yield, for example, would add $218 to the annual economic profit of the fishery in the Vancouver-Columbia area, nothing to the Eureka area fishery, and $533 to the Monterey area fishery. If the harvest constraints could be expanded through biological enhancement, these shadow prices would provide information useful to economic assessment of that enhancement. Since enhancement of groundfish species is generally considered infeasible, however, the shadow price has a different implication. The species with high shadow prices will be those attracting the most competition; they will command the highest prices under a transferable Individual Fisherman Quota system, or will require the closest enforcement effort under other forms of fishery management.

Sensitivity of the results to the joint venture whiting fishery is also shown in Table 6. Without a joint venture fishery and an average pink shrimp fishery, the optimum trawl fleet would have 238 vessels and would generate $7.6 million in profits annually. Adding a 1984-level joint venture fishery increases the optimum fleet to 265 vessels and the annual profit to $11.96 million. If the joint venture fishery grows to take the entire whiting maximum sustainable yield, the optimum fleet would have 338 vessels earning $17.7 million in profits. This wide variation indicates that the

Table 7

Optimum Economic Values when Fleet Is Reduced Sequentially and Size Distribution of Vessels Is Maintained at 1984 Base Level

Trawl Fleet	No. of Vessels	Fleet Profit	Total Revenue	Fixed Cost	Variable Costs	Total Weeks Fished
		$ millions				
1984 Base[a]	429	3.6	73.7	27.5	42.6	10,006
−10%	385	5.5	72.4	24.8	42.1	9,883
−20%	343	6.6	70.5	22.0	41.9	9,885
−30%	301	7.1	66.0	10.3	39.6	9,178
−40%	258	7.3	58.3	16.5	34.5	7,970
−50%	215	7.2	49.8	13.8	28.8	6,641
−60%	171	6.9	40.7	11.0	22.8	5,273
−70%	129	6.5	32.4	8.3	17.6	4,049
−80%	86	5.8	24.3	5.5	13.0	2,921
−90%	44	3.0	12.4	2.8	6.6	1,496

[a] Baseline is 1984 trawl fleet with an optimal allocation of fishing weeks across seasons, areas, and fishing modes.

model's sensitivity to assumed size of the joint venture fishery is quite high. Because the joint venture fishery employs foreign processing vessels, the likely size of that fishery depends on both domestic politics and foreign economic policies as well as domestic economic returns.

As noted above, a practical difficulty with adopting these results for fishery management policy is that the mathematical model ruthlessly ignores existing levels of investment and social commitment to the fishery. Instead of adopting an optimal fleet configuration, fishery managers may prefer to engage in a non-optimal fleet reduction program that improves economic performance with less social disruption. Table 7 examines one such non-optimal program in which the fleet size is sequentially reduced while the size distribution is maintained as initially observed in 1984. The results show that a fleet reduction of 40 percent can achieve a maximum of $7.30 million in economic surplus. This is a $4.7 million reduced profit from the overall optimum. Whether the decrease in social disruption entailed in this second-best fleet reduction program is "worth" the cost of reduced profit is not addressed by this study.

Sensitivity of the mixed integer programming solution to changes in the underlying technological and economic conditions was assessed by running the program with alternative constraints and parameters. The optimum fleet configuration and optimum number of weeks fished are robust to 10 percent changes in fixed costs, but is greatly affected by 30 percent variations. A 30 percent increase in fixed costs reduces the optimum fleet by 45 percent while a 30 percent decrease in fixed costs increases the optimum fleet by 21 percent.

Though it seems reasonable to assume pink shrimp harvests equal to the 1981–82 average of 17,218 short tons, historical fluctuations in the population make it important to assess the sensitivity of the results to variations in the shrimp resource. A 50 percent increase in the pink shrimp catch causes a 22 percent increase in fleet size, while a 50 percent decrease in shrimp causes a 12 percent decrease in optimum fleet size. Fleet profit and distribution of vessels among size classes were little affected. Similarly, the optimum fleet is little affected by 50 percent variations in the crab catch. Other sensitivity analyses show that increasing the maximum weeks of fishing for every size class by one week per season causes a very slight increase in optimum number of fishing weeks and a $1.56 million increase in profit. A combined increase in catch rates of 50 percent for widow rockfish and 30 percent for other rockfish causes only an 8 percent increase in fleet size and a $2.5 million increase in profit.

The results shown in Table 8 demonstrate the importance of maintaining a multipurpose fishing fleet. Columns 1–3 show the optimum vessel numbers, total profit, and weeks fished for three hypothetical specialized fishing fleets. These represent the solutions to three different mixed integer programming models, which assume in turn that the fishing fleet harvests only (1) multispecies groundfish and crab, or (2) pink shrimp, or (3) joint venture whiting (1984 level). Although each of these three separately optimized fleets could be profitable, the sum of the three fleets would contain 105 more vessels, would yield $3.78 million

Table 8

Comparison of Specialized and Multipurpose Optimum Trawl Fleets. Assuming 1984 JV harvest and 1981–82 average pink shrimp harvest.

	(1) Groundfish/ crab only	(2) Shrimp only	(3) JV whiting only	(4) Total for Three Fleets	(5) Change from Multipurpose Fleet[a]
Number of vessels					
Class 1	61	0	0	61	+61
Class 2	36	154	77	267	+87
Class 3	0	0	0	0	0
Class 4	42	0	0	42	−43
Class 5	0	0	0	0	0
Total number	139	154	77	370	+105
Profit ($million)	4.12	.217	3.85	8.18	−3.78
Weeks fished	4,724	3,929	1,449	10,102	+1061

[a] Col. (4) of this Table minus Col. (3) of Table 6.

less in annual profits, and would fish 1061 weeks more than an optimal multipurpose fleet. This result supports the provisional conclusion reported in Huppert (1979) that economically rational fisheries management needs to facilitate the operation of multipurpose fishing fleets. Multipurpose vessels are not only an economically rational adaptation to fluctuating fishing conditions by private operators but they are also economically efficient in aggregate. We conclude that a limited access program seeking to improve economic efficiency and/or fishing profits should not create divisions in the fleet, such as exclusive licensing for groundfish, shrimp, and joint venture whiting fishing.

Summary and Discussion

This mixed integer programming analysis of the Pacific coast trawl fishery yields approximate magnitudes of the economic surplus and fishing fleet size consistent with economically efficient harvest methods. Since the fixed, linear harvest technology specified does not consider possible adjustments in species targeting that would occur under a new management regime, the profit of roughly $12 million represents a lower bound to the potential economic surplus available from the trawl fishery. To achieve this economic surplus for the trawl fleet would require that other gear types be limited to their historic shares of groundfish harvests.

Additional important conclusions are apparent from the mixed integer programming results. First, maximum economic surplus occurs with a trawl fleet that is roughly 38 percent smaller than the fleet existing in 1984 with a 23 percent reduction in weeks fished. The exact size of the optimum fleet depends largely upon the size of the pink shrimp and joint venture whiting fisheries, but is also heavily influenced by variable fishing costs. The optimized fleet would consist of 50–59 ft. and 70–79 ft. trawlers. These results are relatively insensitive to variations in fixed costs, weeks available for fishing per year per vessel, crab catch rates, and rockfish catch rates. The optimum trawl fishery would not fully utilize the available sustainable yields of Dover sole, other flatfish, Pacific cod and ling cod, sablefish or miscellaneous species. It would fully or nearly completely utilize the sustainable yields of widow rockfish, other rockfish, pink shrimp and Pacific whiting to the extent permitted by joint venture fishery.

An important remaining question is whether the estimated surplus value earned under a hypothetical centralized manager could be generated under more traditional forms of economic organization. It is already widely understood that competitive fishing with open access property rules leads to zero net economic value. The estimated annual economic loss of $10 million under our baseline conditions is a reflection of this open access resource characteristic magnified by the rapid fleet expansion of the late 1970s combined with subsequent declines in pink shrimp and rockfish populations. Because of this economic disequilibrium, we would expect the trawl fleet, with or without a new access limitation system, to experience a painful contraction until aggregate fleet earnings return to a break-even level. The adjustment may be very sluggish, however, since the loss of financial capital associated with unprofitable vessel operations does cause rapid physical loss of vessels so long as operating costs can be covered by gross revenues. New owners and new financing arrangements will keep many vessels in operation long after the original owner has written off the investment.

A license limitation program could couple a freeze on new entry with a requirement that replacement vessels be no larger than the original vessels. As license holders retire, attrition could cause the fleet to shrink below the break-even level. Licenses would be issued to new replacement vessels once the fleet achieves an optimum size. Our experiment with this form of license limitation suggests that an optimum economic fleet would be 40 percent smaller than the fleet in 1984 and would earn a little over $7 million in profit. Even this estimate is probably too optimistic. Economic theory and actual experience in the British Columbia salmon fishery (Fraser, 1979) suggest that the emerging fishing profits under a license limitation system will induce fishermen to dissipate profits through costly vessel upgrading. Open access competition for fish would continue among the limited number of operators. Anderson (1985) has argued that a license-limited fishery may settle into an economic equilibrium that does generate positive economic profits, but that these profits will fall short of the maximum possible under a centralized owner/manager.

Individual Transferable Quotas (ITQ) afford a more promising means to generate the potential economic surplus from the trawl fleet. Christy (1973), Moloney and Pearse (1979), and others have argued that an efficiently operating ITQ system could mimic the efficiency of a free market system. This approach would require an altered fisheries law enforcement system and necessitate enhanced legal standing for private rights in fish stocks. New Zealand has recently adopted an ITQ system for deepwater groundfish trawling. Holders of these ITQs will have private economic incentives more consistent with optimum social use of the fishery resources. Such a radical break with traditional fishery systems might entail significant disruptions in private business operations and government bureaucracies. Given the costs of such disruption the potential $12 million harvesting profit may be too small to justify changing the property institutions in the fishery. But the adjustment costs would be transitory, and further investigation of these should precede any decisions on limiting access.

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Potential Economic Benefits of Limited Entry

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In deciding whether to adopt a limited access system, one consideration would be the economic benefits and costs. To pass the benefit-cost test, the potential economic benefits must exceed the total public and private costs of public program implementation. This chapter summarizes the results of an effort to estimate potential economic returns from the groundfish trawl fishery. Chapter 6 presents available information on possible administrative costs.

The economic benefit calculation is abstracted from Huppert and Squires (1986). Benefits from limited access are presumed to occur through increased economic efficiency in fishing fleet construction and deployment. Thus the estimated benefits are derived from a model which calculates, under stated conditions and assumptions, the total fleet profit possible with an optimal fleet size and optimal deployment of fishing effort.

TRAWL FLEET PROFITS

The mathematical model used to calculate potential economic profits is not intended to describe an actual limited access program. Instead, it computes the optimal solution to the fishing fleet construction and deployment problem as though there is a profit-seeking centralized manager of the fishery. This hypothetical manager operates the fleet as if he is starting from scratch. That is, he does not take into consideration the investments sunk into the existing fishing fleet. Therefore, our estimate of maximum economic returns for the fleet is a hypothetical one, describing an ideal result that could be achieved only after a long period of adjustment. We cannot recommend that the trawl fleet be forced into conformance with our computed optimum fleet by a limited access program. This hypothetical model is useful, nevertheless, because it yields a reasonable estimate of what can be achieved in a commercial fishery when the trawl fleet is managed to maximize economic profit.

The Pacific trawl fishery's optimum economic return is computed by linear programming. This procedure calculates the maximum economic profit available to the entire fleet given that the fleet's total catch cannot exceed allowable catch levels. Vessels with non-trawl gear are assumed to continue catching a portion of the total harvest as observed during 1981-84. To implement the linear program, we have to establish catch rates, exvessel prices, and costs of fishing for trawl vessels. Amounts of fishing effort for vessels in each of five length classes are expressed in number of fishing weeks. Each vessel is assumed to be capable of fishing a certain number of weeks during each calendar quarter. Each element of the model has been derived from data collected during the last few years as summarized below.

Allowable catch levels for eight groundfish species and species groups were adopted from the Pacific Fishery Management Council's (1985) estimates for 1985. The proportion of the allowable catches to be taken by the trawl fleet is assumed to equal the average proportion observed during 1981-84. Pacific whiting presented a special problem because it is taken mainly in the joint venture fishery. We examined three different levels for the joint venture Pacific whiting catch centered on the 1984 harvest level. Maximum annual harvest of pink shrimp by trawlers was set at the average 1981-82 total catch (which is close to the recent 12-year average harvest). The average annual trawl fleet catch in 1981-82 was also used to determine the Dungeness crab allowable catch level. Finally, the linear programming model assumes that vessels do not fish more than the typical number of weeks fished by very active trawlers during 1981 and 1982.

The Pacific trawl fishery is considered to have six distinct production processes or fishing modes: (1) mixed-species groundfish trawling in the Vancouver-Columbia area, (2) mixed-species groundfish trawling in the Eureka area, (3) mixed-species groundfish trawling in the Monterey area, (4) single-species pink shrimp trawling, (5) single-species Dungeness crab pot harvesting, and (6) single-species joint venture fishing for Pacific whiting. Eight species categories are caught in the groundfish modes: Dover sole, other flatfish, cod and lingcod, widow rockfish, other rockfish, whiting, sablefish, and a miscellaneous category. The study considers the four calendar-year quarters and five vessel size classes: (1) 40-49 ft., (2) 50-59 ft., (3) 60-69 ft., (4) 70-79 ft., and (5) 80-95 ft. All lengths are Coast Guard registered lengths.

Multispecies groundfish, shrimp, and Dungeness crab catch rates were obtained from the PACFIN research data base (Huppert et al. 1984) maintained at the Southwest Fisheries Center in La Jolla. Average weekly catches for 1981-82 were computed for each fishing mode, area, size class, and season. Catch rates for Pacific whiting joint venture fishing were based upon information from private companies and financial reports. Cost data covering the years 1980-83 were used to estimate average weekly operating costs and annual fixed costs for each length class. Exvessel fish prices were taken from the PACFIN management data base at the Northwest and Alaska Fisheries Center in Seattle. All of these estimates were combined in the program to compute the fleet's profit (gross exvessel value of harvest minus fleetwide operating and fixed costs) for any combination of weeks fished and number of vessels. To provide a baseline for comparison, the prospective fleet profit was calculated for the 1984 trawl fleet while assuming the pattern of fishing weeks observed for the fleet in 1982. This baseline estimate does not correspond to the actual trawl fleet profit in 1984, but it does offer a representative benchmark reflecting the fleet's current economic status.

Table 1 displays a summary of the main results from the linear program. The first column of data in Table 1, representing the baseline 1984 fleet, shows a $10 million loss under the assumed conditions. Columns 2 through 4 report that the trawl fleet could achieve a total profit of between $7.6 and $17.7 million per year depending upon the size of the joint venture whiting fishery. Without a joint venture fishery, the optimum hypothetical fleet would have 238 vessels and would generate $7.6 million in profits annually. Adding a 1984-level joint venture fishery increases the optimum hypothetical fleet to 265 vessels and the annual profit to $11.96 million. Should the joint venture fishery expand to harvest the entire Pacific whiting maximum sustainable yield, the optimum fleet operated by the hypothetical manager would have 338 vessels earning $17.7 million in profits per year. This indicates that the estimated profit and fleet size are sensitive to the assumed level of joint venture activity, an unsurprising result. Because the joint venture fishery employs foreign processing vessels, however, the likely size of this fishery depends upon domestic politics and foreign economic policies as well as standard economic considerations such as the Pacific whiting price and operating costs.

The most reasonable assumption might be that the joint venture fishery remains at the 1984 size. In this case the optimum fleet would enjoy an increase of over $22 million per year from that of a baseline. Slightly more than one-third of the profit is due to multispecies groundfish trawling, about one-quarter comes from shrimp harvesting, about one-quarter is from joint venture fishing of Pacific whiting, and only one-tenth is from crab harvesting.

Table 1—Results of linear programming for the Pacific trawl fleet. JV = joint venture; MSY = max. sustainable yield.

		Optimum fishery[2]		
	Baseline fleet in 1984[1]	JV takes whiting MSY	1984 JV harvest	With no JV fishery
		Number of vessels		
Class 1	106	0	0	0
Class 2	118	245	180	180
Class 3	138	0	0	0
Class 4	55	93	85	58
Class 5	12	0	0	0
Total	429	338	265	238
		Profit ($million)		
	$−10.25	$17.7	$11.96	$7.61
Proportion from[3]:				
Shrimp fishing	0.324	0.180	0.267	0.362
Crab fishing	0.038	0.081	0.109	0.143
Joint venture fishing	0.306	0.475	0.263	0.000
Groundfish	0.332	0.264	0.360	0.495
		Total weeks		
	11,763	11,034	9,041	8,054
Proportion in:				
Shrimp fishing	0.218	0.320	0.380	0.440
Crab fishing	0.044	0.042	0.050	0.060
Joint venture fishing	0.074	0.280	0.130	0.000
Groundfish	0.664	0.358	0.440	0.500

[1] The 1984 baseline fleet does not represent an optimum distribution of fishing weeks. The number and size distribution of vessels represents the 1984 fleet, while the distribution of weeks fished is taken from the 1982 PACFIN research data base (Huppert and Thomson 1985). All prices and costs used in calculating profits are in 1984 dollars.

[2] Various joint venture harvest constraints all assume pink shrimp harvest constraint equals average 1981-82 catch (17,218 short tons).

[3] This is the proportion of operating profit (or net revenue), not economic profit. Fixed costs of vessels are not allocated among fisheries in calculating this proportion.

The size distribution of vessels in the hypothetical fleet operated by a centralized manager differs markedly from the baseline fleet. The optimum hypothetical fleet is composed of 180 vessels in the 50-59 ft. size class and 85 vessels in the 70-79 ft. size class. Absence of the largest and smallest vessel size classes in the optimum fleet is perhaps not unexpected. The surprising absence of mid-sized trawlers in the 60-69 ft. size class in the optimum hypothetical fleet evidently occurs because the greater harvest rates achieved by these vessels, as compared with 50-59 ft. vessels, do not sufficiently counterbalance the proportionately greater increase in harvesting costs.

The analysis does not consider all important aspects of fishing vessel size, however, and these results should not be taken as definitive regarding optimum vessel size. The linear programming approach, for example, does not consider safety, crew comfort, or seaworthiness of the vessels. It also ignores the flexibility that a large vessel may have for cruising to Alaska and for remaining at sea during storms. Relatively small changes in vessel construction or operating cost may cause the linear program to designate that a given size vessel is more

Table 2—Optimum economic values as trawl fleet size is reduced sequentially while maintaining the 1984 size distribution of vessels. Assumes the 1984 level of joint venture whiting catch, and 1981-82 average pink shrimp catch.

	Trawl fleet size	Total fleet profit	Total revenue	Fixed cost	Variable cost	Total weeks fished
		- - - - - -	($millions)	- - - - - -	- - - - - -	
1984 base*	429	3.6	73.7	27.5	42.6	10,006
−10%	385	5.5	72.4	24.8	42.1	9,883
−20%	343	6.5	70.4	22.0	41.9	9,885
−30%	301	7.1	66.0	19.3	39.6	9,178
−40%	258	7.3	58.3	16.5	34.5	7,970
−50%	215	7.2	49.8	13.8	28.8	6,641
−60%	171	6.9	40.7	11.0	22.8	5,273
−70%	129	6.5	32.4	8.3	17.6	4,049
−80%	86	5.8	24.3	5.5	13.0	2,291
−90%	44	3.0	12.4	2.8	6.6	1,496

*Baseline is 1984 trawl fleet with an optimal allocation of fishing weeks across seasons, areas, and fishing modes.

Table 3—Capacity utilization with 10 to 90% reductions in vessel numbers. Assuming 1984 size distribution of vessels, 1984 level of joint venture whiting catch, and 1981-82 average pink shrimp catch.

	Trawl fleet size	Percent utilization				
		Class 1	Class 2	Class 3	Class 4	Class 5
1984 base	429	79.5	81.5	48.3	69.1	0.0
−10%	385	79.5	98.9	53.1	82.4	0.0
−20%	343	100.0	100.0	65.3	100.0	0.0
−30%	301	100.0	100.0	92.2	100.0	0.0
−40%	258	100.0	100.0	75.8	100.0	0.0
−50%	215	100.0	100.0	75.8	100.0	0.0
−60%	171	100.0	100.0	75.8	100.0	0.0
−70%	129	100.0	100.0	80.6	100.0	0.0
−80%	86	100.0	100.0	100.0	100.0	0.0
−90%	44	100.0	100.0	100.0	100.0	0.0

advantageous than another, while in reality decisions on vessel size must recognize these unquantified factors as well as captain's or owner's preferences.

The level and distribution of weeks fished by fishing mode and vessel size class (aggregated over seasons) also differ between the baseline and optimum hypothetical fleets. The optimum fleet's total weeks fished is 9,041, a decline of about 31% from the baseline. All of the fishing time in the optimum hypothetical fleet is concentrated in the second and fourth vessel length classes: 63% in Class 2, and 37% in Class 4. Several other important changes in fishing patterns occur in the optimum hypothetical fleet: the proportion of weeks fished for pink shrimp trawling increases from 22% to 38% of the total; mixed-species groundfish trawling declines by almost one-third; and joint venture fishing for Pacific whiting almost doubles from 7% of the total to 13%.

Further characteristics of the optimum trawl fleet are examined in detail in Huppert and Squires (1986) referenced above. It is shown that the size of this hypothetical optimum fleet is strongly influenced by the size of the pink shrimp fishery. Also, the conclusions are relatively insensitive to variations in fixed costs, weeks available for fishing per year, and catch rates for Dungeness crab and rockfish. The optimum hypothetical fishery would not fully utilize the available sustainable yields of Dover sole, other flatfish, Pacific cod and lingcod, sablefish, or miscellaneous species. It would fully or nearly completely utilize the sustainable yields of widow rockfish, other rockfish, pink shrimp, and Pacific whiting to the extent permitted by the joint venture fishery.

As noted earlier, these results are pertinent to a hypothetical fleet manager who does not have to deal with the existing trawl fleet. Given the current number and size distribution of trawlers, a manager might suboptimize by deploying the existing fleet's fishing weeks across seasons, areas, and fishing modes. As depicted in the first row of Table 2, this restricted profit maximization generates an annual fleet profit of $3.60 million. The hypothetical central manager might try to expand annual profit by reducing the number of vessels through attrition. We assume that attrition reduces all size classes in proportion. As shown in Tables 2 and 3, the fixed and variable costs of fishing would fall faster than the total revenue earned as the fleet is reduced up to 40% from the base 1984 level. The maximum fleet profit through this attrition program is only $7.3 million.

In evaluating the attrition program, we require that the hypothetical manager pay the fixed costs of maintaining the prescribed fleet, but we do not require that all vessels actually be deployed in the fishery. Some vessels may well be treated as surplus capacity and tied up to the dock. Table 3 shows the percent utilization of the total fishing weeks available to the manager with each fleet size. In particular, this shows that the Class 5 vessels are so uneconomic that they would not be used even though the manager is charged the substantial fixed cost for interest and depreciation. If the Class 5 vessels were not in the fleet, revenue from harvests would be unaffected, but the cost would be reduced by $110,550 per vessel. Without Class 5 vessels, the annual fleet profit would rise to $4.9 million with the 1984 base fleet, and to $8.1 million with a fleet reduced by 40%.

The current fleet is a multipurpose fleet composed of trawlers which, depending upon conditions, might target mixed-species groundfish, pink shrimp, Dungeness crab, or Pacific whiting through joint venture operations. The set of results presented in Table 4 demonstrates the economic importance of maintaining a multipurpose fleet. Columns 1-3 show the optimum vessel numbers, total fleet profit, and weeks fished for three hypothetical specialized fleets harvesting (1) only multispecies groundfish and crab, (2) only pink shrimp, and (3) only joint venture Pacific whiting at the 1984 level. Each of these three separately operated fleets could be profitable. Yet, the sum of the three fleets would contain 149 more vessels, would yield $3.78 million less in annual profits, and would fish 1,061 weeks more than an optimal hypothetical multipurpose fleet. This result suggests that a limited access program seeking to improve fleet profits should not create divisions in the fleet based upon exclusive licensing for groundfish, pink shrimp, and joint venture Pacific whiting fishing.

In summary, the analysis of the Pacific coast trawl fishery suggests a maximum fleet annual economic profit of around $12 million. This represents the total profit that might be attained by a hypothetical central manager designing a new trawl fleet. The maximum economic surplus from this hypothetical fleet occurs with a trawl fleet about 38% smaller than the fleet existing in 1984, with a 23% reduction in weeks fished. Without altering the size distribution of vessels, a reduction of about 40% in the trawl fleet would yield a profit of around $7 million, again assuming the fishing weeks are optimally deployed among seasons, fishing areas, and fishing modes.

Table 4—Comparison of specialized and multipurpose optimum trawl fleets assuming 1984 joint venture (JV) harvest and 1981-82 average pink shrimp harvest.

	Specialized fleets				
	Groundfish/ crab only	Shrimp only	JV whiting only	Total	Change from multipurpose fleet
	Number of vessels				
Class 1	61	0	0	61	+61
Class 2	36	154	77	267	+87
Class 3	0	0	0	0	0
Class 4	42	0	0	42	−43
Class 5	0	0	0	0	0
Total	139	154	77	370	+105
	Profit ($million)				
	$4.12	$0.217	$3.85	$8.18	$−3.78
	Weeks fished				
	4,724	3,929	1,449	10,102	+1,061

NON-TRAWL FLEET

If the entire groundfish fishery is placed under a limited access system, the potential profits would be somewhat larger than that estimated for the trawl fleet alone. During the base period of 1981-84, the fixed gear fleet took the following portions of the total Pacific coast groundfish harvest: 12% of cod and lingcod, 6% of other rockfish, 42% of sablefish, and 7% of the miscellaneous fish. Assuming that the fixed gear fleet would continue to take these portions of the total allowable catches, and that it receives the same exvessel prices as trawlers, the non-trawl gross revenue would be about $3.5 million. Without incorporating non-trawl fishing cost information, we cannot accurately estimate the level of profits that this would generate.

As a first approximation, however, we could assume that profits would be the same percentage of gross revenue (i.e., total exvessel value of harvests) for fixed gear as for trawlers. For the trawl fleet as a whole, profits would be about 17.5% of gross revenue for the optimum fishery. Our corresponding educated guess of non-trawl groundfish profits would be about $605,000.

IMPLICATIONS FOR LIMITED ACCESS

The total potential economic profit of $12.6 million represents an annual commercial profit under very specialized conditions. This is a useful rough assessment of net economic benefit attributable to the harvesting of commercial groundfish. It is not clear, however, that this is a reasonable assessment of potential benefits from limiting access to the fishery. There are two main concerns. First, achievement of this total profit requires a trawl fleet that is substantially different from the fleet existing today. But any real limited access program must begin with today's fishing fleet. Also, without detailed consideration of several additional vessel design factors, one cannot be very confident that these particular changes in vessel size distribution will be as beneficial as the model predicts. Second, the practical means of limiting access cannot literally mimic the centralized decision-maker concept, and hence cannot necessarily result in the level of fleet profits calculated. License limitation, for example, would not result in the optimal deployment of fishing effort that the mathematical model recommends. To achieve the economically optimal deployment across species, areas, and seasons, either the manager must wield incredibly detailed direct control over the fleet or the independent vessel operators must have economic incentives that lead them to the optimal solution. Discussion of these two concerns should place this chapter in proper perspective.

Any limited access system likely to be adopted in a commercial fishery would undoubtedly begin by "grandfathering in" the existing fishing fleet. Thus the optimum vessel numbers and size configuration would not be adopted immediately. A more reasonable estimate of potential profit would be the $7.3 million shown in Table 3. Adding the non-trawl profit to this gives us an estimate of about $8 million per year. This is our current best estimate of the size of potential profits from the fishery under the conditions assumed by our mathematical model.

The second concern is that practical limited access systems may not be able to approximate the optimum fleet management assumed in the model. Experience with license limitation programs, for example, shows that limiting numbers of vessels or fishermen does not effectively limit the level of fishing effort, nor does it necessarily lead to an optimal redeployment of effort to maximize overall economic benefit. Increased investment in fishing capacity by licensed vessels can cancel out the capacity-reducing effects of limiting number of participants, and this will cut into the potential profit. Various restraints may be placed upon fishing capacity in order to prevent this from happening. Improvements in fishing technology, comfort, and safety aboard commercial vessels, however, will all involve capital investments. In the long run we cannot prevent these changes in order to preserve economic profits. Thus it is difficult to imagine a license limitation program that would preserve both economic profits and technological progressiveness.

Of equal concern is the conservation effect of excess fishing effort. Even though their numbers may be limited, the fishing fleets for salmon, halibut, and herring roe (to name just three examples) must be further restricted in order to conserve fish stocks. As explained in Chapters 1 and 4, the limit on licenses helps to create a group of common resource users who may coordinate their actions to optimize the resource harvest. But the act of limiting membership to the group of harvesters does not immediately assure the high degree of cooperative behavior needed to achieve optimum results. The kinds of restrictions placed upon fishing fleets to restrain fishing effort in these circumstances often cause increases in fishing costs. Again, this would prevent the fleet from achieving the potential economic profits. It seems more likely that quantitative harvest rights systems, such as New Zealand's Individual Transferable Quotas (ITQs), will succeed at meeting the multiple economic objectives of an efficient harvesting industry. But there are potential problems with the ITQ system as well, including enforcement and control of discards. Thus the economic benefit estimates developed in this chapter should be taken as a sort of target level which may or may not be achievable with a practical limited access program.

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3

Elements of a Limited Access Program

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This section presents the basic "nuts and bolts" of limited access, carrying the discussion of limited entry beyond the general considerations reviewed in previous sections to look at specific elements. A proposed checklist of items for consideration, along with a brief description of the main options is presented in Figure 1 below. Seven basic decision categories are:

(1) Scope of the fishing activity to be restricted or allocated
(2) Method of limiting access
(3) Initial allocation of harvest rights
(4) Transferability of harvest rights
(5) Longevity of harvest rights
(6) Mechanisms for adjusting the number of harvest rights
(7) Handling disputes regarding issuance and transfer of rights.

In the absence of limited access to the fishery, any U.S. resident who pays the appropriate fees to State authorities has a right to fish for groundfish. This right is circumscribed by the various restrictions on commercial gear (e.g., trawl net minimum mesh size), by fishing season closures, by "trip limits," by incidental catch allowances, and prohibitions on retaining salmon and halibut. There is no legal restriction, however, on who can participate at any given time or place, and no specific restriction on the amount that any individual can legally land during a given fishing season. Thus, while there are many restrictions on fishing practices, current fishing rights are unlimited in number, unrestricted in total harvest amounts, and very inexpensive for the individual to maintain.

The discussion of elements in Figure 1 will focus on a trawl license limitation proposal developed in November 1984 by the Fisherman's Marketing Association and Coast Draggers Association (FMA/CDA) (see Appendix A). Although that proposal is called a moratorium, it has the essential features of a license limitation program. Of interest here is the contrast between the features outlined in that specific proposal and the alternatives listed in Figure 1. We will proceed through each of the seven categories.

SCOPE

The FMA/CDA proposal envisions a relatively narrow scope for the license limitation program in some respects (limited to trawl vessels) and a rather broad scope in other respects (covers entire coast and all species of groundfish listed in the management plan (Pac. Fish. Manage. Counc. 1982)). It leaves out all other commercial gear types and recreational fishing. Except in southern California, the recreational component of groundfish catch is too small (and will probably remain too small) for this exemption to matter much. Ignoring other gear types, however, is a more substantive deletion. Although trawl gear dominates the total catch, gillnet fishing is apparently on the rise and may portend greater competition for fish and space in the future. One strength of this approach is that it limits the most important element of the commercial fleet while minimizing the number of individual fishing operations that must be regulated.

By including all groundfish species and all fishing sites on the west coast, the FMA/CDA proposal would preserve great latitude in trawl fishing operations. Trawl vessel operators have suggested that they need to have many options open to them under any regulatory system. Geographic area and fish species availability are two dimensions to these "options," but there are others. For example, with a large fishing fleet and great latitude in fishing

Figure 1—Limited Access Program Elements and Options

I. Scope of fishing activities to be restricted or allocated

A. Types of fishing to be included	1. All commercial and recreational
	2. All commercial plus for-profit party and charter boat fishing
	3. All commercial fishing
	4. Only "big-time" commercial operations, such as those landing at least 50 tons of groundfish per year.
B. Geographical extent	1. All Pacific coast including at-sea sales
	2. All Pacific coast shoreside landings
	3. Pacific coast shoreside harvests from the 3-200 nautical mile zone (FCZ, excluding state waters).
	4. Harvests in certain selected INPFC areas such as the Vancouver or Columbia areas.
C. Fishing gear types	1. All gear including groundfish trawl, hook and line, fish pots, gill nets, and shrimp trawls.
	2. Control only "directed" fishing with trawl gear, fish pots, and gill nets.
	3. Control only the major gear type—trawls (see FMA Proposal Appendix A).
D. Species of fish	1. All species listed in groundfish fishery management plan (Pac. Fish. Manage. Counc. 1982).
	2. Include only "important" groundfish species (e.g., all rockfishes, whiting, sablefish, Dover sole, English sole, petrale sole, Pacific cod, ling cod).
	3. Focus harvest permits or rights on single species or logical groups of species. For example, a "rockfish" permit or a "whiting" joint venture permit.

II. Means of limiting access to the fishery

A. License limitation	1. Personal License to fish (with or without limiting to "natural persons").
	2. License attached to vessel
	3. License attached to gear (e.g., net)
	4. Dual system: fishing license for people plus vessel or gear permits.
B. Individual fisherman quota (IFQ)	1. IFQ conveys right to take a share of the allowable yield of specific stocks.
	2. IFQ conveys right to take annually a specified quantity from a specific stock.
	3. Annual yield is assigned to a company or fisherman's cooperative to be subdivided among fishermen. ("Enterprise quotas")
C. Taxes, royalties and fees	1. Set initial entry fees high enough to discourage excessive participation.
	2. Establish landings royalties for fully utilized species.
	3. Establish annual license renewal fees.

III. Basis for initial allocation of harvest rights

A. Administrative assignments	1. Include all persons or firms with recent record of landings (e.g., landed at least one fish in the past five years).
	2. Include all applicants within a specified time period.
	3. Include all persons or firms meeting minimum landings requirements.
	4. Hold a lottery among all applicants.
	5. Include all persons meeting certain qualifications as commercial fishermen.
B. Competitive market allocation	1. Auction off limited number of fishing licenses or IFQs.
	2. Sell licenses or IFQs at prices calculated to reflect market values.

IV. Transferability

A. Nontransferable	1. Retirement or death causes termination of fishing license or harvest right; may revert to State to be reissued.
	2. Ownership transfer not allowed, but owner may lease or lend fishing right.
B. License or IFQ attached to specific vessel or gear	1. Transfer requires sale of vessel or gear.
	2. May be transferred among vessels of equal fishing capacity.
	3. May be subject to clearance by State and qualification of new owner.
C. Fully transferable at discretion of owner	1. Market sales may be subject to clearance by State fisheries agency or review board.
	2. State may require that new vessel have no more harvest capacity than previously licensed vessel.

V. Duration of term of fishing right	1. Perpetual. The license or IFQ can be used as long as the owner wishes.
	2. Annual, renewable or nonrenewable. Renewal could be automatic or could depend upon continued participation in fishery.
	3. Dependent upon lifetime or career of permit holder. License or right expires upon death or retirement of holder.
	4. Fixed, multiyear term. License or IFQ might confer right to fish for, say, 10 years.

VI. Means of altering number of licenses or fishing rights

A. Fleet reduction	1. Attrition through retirement, termination, revocation for cause.
	2. Buy-back of perpetual or long-lived licenses by State or Federal agency.
	3. Automatic expiration of fixed-term licenses in conjunction with issue or sale of reduced number of new licenses.
B. Increase in number licenses or rights	1. Lottery among "qualified applicants".
	2. Sale to applicants at agency-established price.
	3. Selection of new licensees on first-come, first-served basis.
	4. Auction of new licenses or rights in competitive market open to all.

VII. Settling disputes regarding issuance and transfer of fishing rights

A. State/Federal Court	Fishermen can ultimately seek redress in the courts under any of the options.
B. Administrative Law Judge (ALJ)	1. ALJ could make a final administrative ruling after hearing with fisherman.
	2. ALJ could make recommendation to agency administrator after hearing issue.
C. Special Appeals or Review Board	1. A board of peers (industry representatives) could make rulings or recommendations to agency administrator.
	2. A board of disinterested citizens could hear disputes.
D. Agency Administrator	1. Administrator could make final rulings for agency (e.g., NMFS Regional Director).
	2. Administrator could be bound to pass issue to Federal department head.

options, current fish stock conservation regulations have limited the ability of trawl vessels to choose timing and quantity of rockfish to catch by imposing trip limits and season closures.

Three alternatives to the FMA/CDA proposal meriting consideration are (1) including all gear types in the license limitation program, (2) limiting the scope to "major" groundfish species, and (3) permitting small catch levels by unlicensed vessels. Extension to all gear types would increase the size of the licensed fleet by an order of magnitude, but would bring the various fixed gear vessels under control early. This would address the potential future problem of expanding harvest capacity by an unregulated portion of the fishing fleet. Second, the idea of licensing only those vessels fishing "major" species would alleviate the need to include in the limited fleet every vessel that catches an occasional spiny dogfish or soupfin shark. Without restricting the program to major species, the extension to all gear types would undoubtedly make the system too all-inclusive and cumbersome.

A third option might be to allow unlicensed vessels to land groundfish below a certain limit. All unlicensed vessels could be allowed, for example, to land up to 1,000 pounds of groundfish on any trip, or up to 10,000 pounds per year. This would permit the minor incidental catch of groundfish by trollers, shrimp vessels, and purse seiners without adding these vessels (and the redundant harvest capacity they might represent) to a permanent licensed groundfish fleet.

MEANS OF LIMITING ACCESS

The FMA/CDA proposal is for a groundfish fishing license attached to the vessel. The principal alternative form of licensing, the personal fishing license, has been adopted in Alaska and elsewhere. The choice between these two license alternatives should have some effect on relative bargaining strengths of vessel owners and fishermen. With personal licenses limiting the number of people who can legally fish, ownership of capital equipment is not a prerequisite for ownership of fishing rights. In the Alaska salmon case, personal fishing licenses cannot be used as collateral for loans and cannot be owned by corporations. These provisions were supposed to protect licensed fishermen from some possible threats to their continued participation in the fishery. Vessel owners might object to this because their ability to continue receiving income from a capital investment would depend upon success in recruiting a licensed crew.

Choice between attachment to individuals or vessels must be made in designing IFQs as well. If the 10,000-ton allowable bycatch for sablefish were allocated as 500 20-ton IFQs, these could be assigned on the basis of historical share to fishermen, to vessel owners, or even to corporations involved in fish processing. With personal IFQs, a trawl vessel owner would need to hire a skipper or crewmember holding an IFQ; with share assigned to vessels the owner would have control of the harvest right and fishermen not owning vessels would be at a disadvantage; and with corporate ownership of shares the processors could more easily plan and manage the fleet fishing for them.

A sub-option for IFQs is partial implementation of the system for a subset of groundfish stocks. One could allocate the estimated annual allowable catch of widow rockfish, sablefish, or Dover sole while leaving other species out of the IFQ system. Also, as suggested by Robert Stokes (1983) in his study of north Pacific halibut, one could establish IFQs for a portion of the total harvest of a given species while retaining a communal fishery for the remainder of the harvest. This option has the advantage of providing a choice to fishermen who, for whatever reason, do not want to join a quantitative rights system. If one-half of the traditional harvesters of Dover sole object to an IFQ system, one could distribute IFQs for half the annual yield to those wishing to join the system. The traditional harvest sector would fish from January 1 until one-half of the annual allowable bycatch is taken. Fishermen with IFQs could fish whenever they wish, and would probably time their harvest to maximize its landed value.

INITIAL ALLOCATION OF FISHING RIGHTS

The FMA/CDA proposal would allocate trawl licenses only to certain groundfish trawlers (1) landing at least 100,000 pounds or (2) making at least 12 deliveries during 1984 or (3) demonstrating to an industry-governing Board that they had prior involvement in the fishery and were active in the north Pacific or Bering Sea trawl fishery in 1984 or (4) demonstrating to the Board that they signed a contract or began construction or conversion of a trawl vessel during 1984. These qualifications would exclude very few groundfish trawl fishing vessels from the licensed fleet. For that reason, this initial allocation of harvest rights would create no significant reduction in harvesting capacity.

Whether licenses or IFQs are considered, the basic choice here is between administrative assignment and some kind of "market allocation." Administrative assignments are universally chosen in existing limited access programs, largely because government agencies (and legislators) are reluctant to take away historically established fishing rights. As noted in the Introduction, when government regulations are designed to correct technical problems of communal resource usage, use rights are generally assigned to actual, historic users in order to avoid causing a redistribution of wealth. However, when developing new resources (offshore oil) or distributing public resources not previously used (National Forest timber), government mechanisms tend to use more market-oriented allocations (auctions and royalties) which extract resource value from the users.

A case could be made that both historic use and new uses are found in the Pacific groundfish fishery. Extensive historic use of most flatfish, rockfish, and sablefish by commercial fishing fleets could establish an informal "ownership" of the right to harvest. At the same time, however, new or developing fisheries have no such specific historic use. Pacific whiting, shortbelly rockfish, sanddabs, and possibly other groundfish stocks would be essentially "new" from this perspective. A mix of administrative and market allocation of initial harvest rights could be justified on this basis. Ultimately, there is no technically correct answer to the initial allocation question. Distribution of public resources can and has been done in many ways.

TRANSFERABILITY OF HARVEST RIGHTS

Under the FMA/CDA proposal, the trawl licenses would be transferred with sale of the vessel and could be shifted from one vessel to another by the owner if the licensed vessel is lost or if the owner wants to "upgrade" or "downgrade" his vessel. Although the license itself would not be saleable under this system, it would be fairly easy to perform almost any kind of transfer. For example, if a licensed vessel owner wants to take his vessel to a different fishery, he could replace his vessel with another and then sell the new vessel with license. Or, he could sell the original vessel with license to another fisherman, who would then replace the vessel and sell the original vessel back to the original owner. There would be no apparent market value to a license, but the difference between vessel prices with and without a license would provide a good indication of license value. The restriction on sales simply makes transactions involving limited harvest rights a cumbersome and roundabout process.

An alternative to this is a fully saleable license. If sufficient numbers of licenses or quantitative harvest rights (IFQs) change hands on a routine basis, the market allocation of fishing rights would have all the advantages and disadvantages of market allocations that are experienced in sectors of the economy. Market allocations are presumed to facilitate the efficient entry and exit of resource users. Less adept or profitable harvesters would be encouraged to sell their rights and enter a different line of work, while more efficient operators could expand. No coercion would be necessary, since anyone with a license or harvest right would have the option of not selling.

With vessel licenses as proposed by FMA/CDA, sufficient transferability seems to be incorporated. For an IFQ system to work, however, true market sales would be almost a necessity. One alternative is for annual harvest quotas to be initially allocated among vessel owners in proportion to their historic shares. A vessel owner with a vessel that breaks down for an extended time would want to sell any quotas he owns to another operator. Also, a vessel which is harvesting mostly rockfish may want to shift into shrimp or Dover sole fishing. The owner will need to sell one set of quotas and buy a new set. Without the freedom of market sales, it would be difficult to maintain operating flexibility with quantitative harvest rights.

LONGEVITY OF HARVEST RIGHTS

In view of the long-lived investments inherent in both fishing vessels and fishing know-how, there seems to be no logical reason for licenses or IFQs to expire annually or over a short period of years. The FMA/CDA proposal allows perpetual trawl licenses. Only if a vessel owner fails to meet minimum landing requirements and fails to seek an exemption for his vessel, would a license be automatically retired. Personal licenses in Alaska and elsewhere are also perpetual. The Pearse Commission recommended that British Columbia salmon licenses be issued for a 10-year term, but that proposal was part of an intended fleet reduction program that would end with issuance of a smaller number of perpetual licenses.

In a limited access program incorporating all gear types, however, it might be useful to issue short-term licenses to vessels that really intend to fish only for a short time or which temporarily exceed some maximum harvest level allowed for unlicensed vessels. With a fully marketable IFQ system, anyone wanting to temporarily enter or leave the groundfish fishery would have the opportunity to do so.

MECHANISMS FOR ADJUSTING NUMBERS OF HARVEST RIGHTS

Under the FMA/CDA proposal, the number of trawl licenses, once established, would change only where individual owners allowed their licenses to lapse. Because these licenses would be potentially valuable in the future, it would be unlikely that significant numbers of vessel owners would voluntarily withdraw from the licensed fleet. Assuming that there will be slow attrition from the trawl fishery, the FMA/CDA proposal calls for an annual review of the size and condition of the fleet. No specific procedures are included, however, for either causing more rapid decrease in the fleet or for increasing the number of licenses at some future time.

To achieve an economically efficient fleet size, some reduction in number of vessels would be necessary under a license limitation program. On the other hand, an expansion of the currently developable fisheries for Pacific whiting and shortbelly rockfish might justify adding to the fleet.

For fleet reduction, attrition and buyback programs are the only frequently discussed alternatives. For attrition to have much effect, there must be fairly stringent annual requirements for renewal of licenses, and the licenses must not be transferable to new fishermen. This approach, therefore, seems to impose a rather arbitrary distribution of fleet reduction burden among fishermen. Also, while waiting for attrition to take its toll, many fishermen may be led to remain in the fishery when they should not for health or safety reasons.

Buyback of vessel licenses provides a positive means of reducing the number of vessels, but it requires a source of funding. In their extensive review of buyback of fishing rights, Schelle and Muse (1984) found only one that was not a government subsidized program. If Congress and state legislatures are not prepared to provide financing, then fees and royalties from the fishery could be used to create a fund for buyback. A large number of technical issues need to be addressed in designing a buyback system, including (1) determining the target fleet size, choosing (2) whether to buy licenses only or to include vessels and gear, and (3) whether to target the buyback on a specific distribution of vessel sizes and capacities, and (4) determining the specifics of the application and offer system.

One innovative means of reducing vessel numbers was implemented in the British Columbia roe herring license system. The fishery was divided into three sub-areas and each licensed fisherman was allowed to choose one area. Licenses are saleable, however, and a license owner may buy up licenses from all three areas. If management authorities stagger the openings of herring fishing seasons in the three areas, this method of fleet reduction allows consolidation of fishing operations with attendant reductions in fishing costs. Potentially, the total number of participants could fall to one-third the original number. In fact, from 1981 to 1985 the total number of licenses fell from 1,557 to 1,132. As of 1985, only 17 vessels had three licenses. P. MacGillivray (1986) notes that the British Columbia system resulted in both improved product quality and reduced fishing costs.

Under an IFQ system, numbers of participants need not be adjusted directly. Instead, the quota initially allocated will be redistributed in private market transactions to determine the number of participants. With marketable IFQs, adjustment of numbers of vessels or fishermen is not administered by the management program. Nevertheless, ownership of IFQs may be restricted to some defined class of "qualified" fishermen, and the number of such fishermen may be of concern. It is difficult to anticipate what issues might arise under such a system in the absence of any experience with it or a specific proposal.

HANDLING DISPUTES

Disputes are likely to arise concerning the initial allocation of harvest rights (whether licenses or IFQs), and in exercising the mechanisms for license transfer, renewal and termination. Most existing license limitation programs avoid disputes regarding initial allocation by including almost every conceivable claimant. Alaska's salmon license program did not, much to the chagrin of the Commercial Fisheries Entry Commission. The Alaska system required the Entry Commission to establish means of determining the extent to which applicants met various criteria concerning historic participation and dependence on the fishery. Challenges to the Commission's procedures and decisions still, after 10 years of operation, constitute a significant portion of the Commission's business. This could be avoided by establishing quantitative criteria in law or regulation at the outset, rather than leaving interpretation of some vague criteria to a quasiregulatory body.

To deal with the disputes that occur, several alternative procedures could be established. A review board dominated by fishermen and other industry members could decide whether individuals should be given licenses and whether proposed license or vessel transfers should be allowed. A variant on this is to use the board to make recommendations to an agency administrator (e.g., an NMFS Regional Director) who would make an official ruling. Fishermen affected by decisions of the Board may feel that they will get a more sympathetic hearing before their peers than before a nonfishing administrative or judicial panel. On the other hand, both fishermen and the public-at-large occasionally may fear that conflicts of interest or favoritism are more likely to affect the decisions of an industry-dominated review board.

Other approaches could include use of an Administrative Law Judge to hear evidence and make recommendations or rulings. Agency administrative procedures could be used to hear grievances and make rulings. In any case, a fisherman has access to the courts to seek redress of arbitrary or wrongful actions by the management agency.

CONCLUSIONS

A tremendous variety of combinations of limited access program elements can and have been attempted. This chapter has introduced and explained many of the most commonly discussed alternatives under seven categories. Further innovation in developing variants on these alternatives will surely be an activity for fishermen, managers, and scientists involved in limited access programs.

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EFFECTS OF SAMPLE SIZE AND CONTAGION ON ESTIMATING FISH EGG ABUNDANCE

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ABSTRACT

Because pelagic fish eggs are usually distributed contagiously, the mean and variance estimated from egg surveys are often driven by a few samples of very high abundance. "Sampling" from simulated negative binomial data sets ($n = 20$ to 1,000, $k = .1$ to .4) showed that the sample mean and variance were both highly dependent on the maximum observed value. As contagion (k^{-1}) increased, or n decreased, the chance of a sample including rare, high values decreased. In consequence, nominally 95% confidence limits excluded the population mean more than 5% of the time and tended to underestimate the mean more often than to overestimate it. Log-based parametric estimates were superior to those assuming a normal distribution of sample means, but only at $k = .4$ and $n \geq 500$ did the error rate approach 2.5% in both tails. Since contagion in pelagic fish egg distributions is often greater than this ($k < .4$), and affordable sample size usually small ($n < 1,000$), a method was sought that would improve accuracy by increasing the asymmetry of confidence bounds. One potential methodology is Easterling's "consonance regions," applied here to samples from a large set of *Engraulis mordax* egg data.

RESUMEN

Debido a la distribución contagiosa de los huevos de peces pelágicos, el promedio y la varianza estimados de recuentos de huevos son a menudo determinados por un bajo número de muestras con alta abundancia. Los "muestreos" de varios conjuntos de datos simulados de distribución binomial negativa ($n = 20$ a 1000, $k = 0.1$ a 0.4) indican que el promedio y la varianza de la muestra son ambas altamente dependientes del máximo valor observado. A medida que el grado de contagio (k^{-1}) aumenta o n disminuye, la probabilidad que una muestra contenga valores altos, de baja frecuencia, disminuye. Consecuentemente, los límites de confidencia del 95% excluyen el promedio de la población en un 5% de los casos y tienden, en general, a subestimar el promedio. Aun cuando las estimaciones paramétricas con distribución logarítmica resultaron ser superiores a aquéllas para las cuales se supuso una distribución normal, el error alcanzó únicamente un 2.5% en cada cola cuando $k = .4$ y $n \geq 500$. Dado que el grado de contagio en las distribuciones de huevos de peces pelágicos es generalmente mayor ($k < .4$), ye el tamaño de muestra es generalmente pequeño ($n < 1000$), se buscó un método que mejorara la exactitud por medio de un aumento en la asimetría de los límites de confidencia. El método de Easterling o "método de regiones consonantes" ha sido usado en este trabajo con muestras provenientes de un alto número de datos de huevos de *Engraulis mordax*.

INTRODUCTION

The usual method of computing confidence intervals rests on the assumption that the distribution of (theoretical) sample means is normal (i.e., that the central-limit theorem applies). Robust as this assumption is, the patchy distribution of fish eggs and larvae can give rise to sufficient contagion in survey data to cause significant departures (e.g., the mean of northern anchovy egg samples of $n < 60$ tends to be skewed).

Although statistics texts treat the problem lightly, if at all, proposals for measuring precision in contagious data do appear in the fisheries literature (e.g., Taft 1960; Zweifel and Smith 1981; Pennington 1983; Pennington and Berrien 1984; Jahn, in press). All the proposed methods deal in some way with the asymmetric distribution of sample means, but little has been done to quantify the error rates inherent in each. This has moderate consequences in most fisheries applications, because sample size is typically held large to counteract the effects of contagion and achieve good precision. However, in research that enjoys less financial support, such as environmental impact studies, sample size is often set by factors external to the nature of the variability and is nearly always smaller than the investigator would wish for.

For a given level of abundance, the definition of "small" sample size depends on the desired precision and the degree of contagion. In this paper we demonstrate the interdependence of estimated

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mean and variance, and use simulation to quantify the actual precision obtained from such estimates over a range of sample sizes and degrees of contagion common in coastal ichthyoplankton work. The simulation results, based on completely specified negative binomial distributions, are compared with samples from large "populations" of real anchovy egg data. We also briefly explore an alternate method of estimating precision that shows promise for small samples.

METHODS

Statistics

Skewness ($g1$) and kurtosis ($g2$) were calculated according to procedures in Sokal and Rohlf (1969). Formulas used in computing parametric confidence limits were:

$$m \pm t_\alpha \cdot \mathrm{SE} \tag{1}$$

$$m \cdot \exp\{\pm\, t_\alpha \surd\, [\ln(1 + \mathrm{SE}^2/m^2)]\} \tag{2}$$

where m is the sample mean, t_α the standard normal deviate (here approximated as = 2), and SE the standard error of the mean. Formula 1 is the familiar method, which assumes a normal distribution of m. Formula 2, from Zweifel and Smith (1981), assumes the log-normal distribution of m.

Another method explored was the procedure of simultaneous model fitting and parameter estimation suggested by Easterling (1976), in which an array of parameters is employed in goodness-of-fit tests to define a two-dimensional region in which the data are consonant with the specified model. A full description of this procedure, as applied here using the negative binomial frequency distribution and x^2 goodness-of-fit tests, is given in Jahn (in press).

It should be said at the outset that Easterling's proposal was not specifically for making population inferences, but rather for obtaining an objective description of data. Our motivation for applying the technique to a problem of inference was that it produces an asymmetry of fiducial limits that has the desired properties for small samples from contagious distributions. Easterling (1976) has shown that, for a given probability level, consonance regions will tend to be wider than parametric confidence intervals, the difference depending on the nature of the data. We have found that, with small sets of ichthyoplankton data as treated here, a probability of 0.2, or an 80% consonance region, gives an interval of comparable size to a 95% confidence interval, but with more appropriate asymmetry, as will be shown.

Simulations

To obtain an empirical estimate of the accuracy of parametric confidence limits, "sampling" was carried out on three simulated data sets, each distributed as a negative binomial completely specified by the parameters m (the mean, set = 10 in all cases) and k (an inverse contagion parameter, set = 0.1, 0.2, and 0.4). The simulated populations, generated according to procedures given in Elliott (1971), consisted of 50,000 numbers each, sufficient to produce variances > 99% of asymptotic values ($s^2 = m + m^2/k$). From each population, 1,000 random samples of n = 20, 50, 100, 200, 500, and 1,000 were taken, and their mean, variance, and maximum value recorded.

Egg Data

Real fish-egg abundance data came from surveys employing a 0.05 m^2 vertically towed net, the CalVET sampler (Smith et al. 1985). The six CalVET surveys for 1980–85 took 5,338 samples, of which 2,311 were positive for northern anchovy (*Engraulis mordax*) eggs. Ages of all eggs from each sample were estimated from stage of development and field temperature (Lo 1985). For subsampling purposes, the 3,027 (5,338 − 2,311) negative stations were considered outside the spawning area and omitted as "false" zeros[1]. The first (A) and second (B) whole days after spawning, and total eggs (T), were the three "populations" from which random subsamples of n = 20, 46, 100, 200, and 500 were taken. The two smallest sample sizes correspond to the number of samples per cruise in a program of nearshore egg and larval surveys, wherein mean abundances have been reported with various measures of precision, including some methods used here (Brewer and Smith 1982; Lavenberg et al. 1986; Jahn, in press).

RESULTS AND DISCUSSION

Simulations

For a given level of contagion, the range and symmetry of the distribution of sample means were (as expected) strongly related to sample size (Figure 1). The width of the range of the central 95% of sample means was well predicted from population parameters as 4 standard errors of the mean

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[1] By "false" zeros we mean that these observations were taken outside the spawning area and not by chance from within it. (For a more thorough treatment see Smith 1973.) This oversimplification will have slight consequences for the biological character of our example data sets, but the allocation of zeros is a problem in fisheries practice that rivals that of precision.

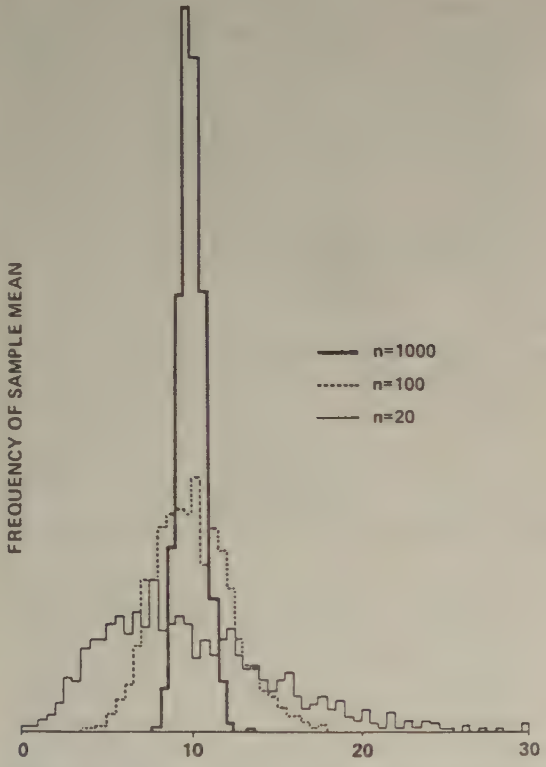

Figure 1. Superimposed histograms of 1,000 sample means for three sample sizes from a negative binomial population with $m = 10$, $k = .2$.

(approximated as $4\mu/\sqrt{kn}$, Table 1), but this interval was never precisely centered on the population mean. The asymmetry of the interval [(upper limit $-\ \mu)/(\mu\ -$ lower limit)] varied inversely with both n and k (Table 1 and Figure 2). Although the distribution of sample means is interesting and informative in a theoretical context, the real problem in practice is estimating population parameters from the information contained in a single sample.

For all three simulated populations, as in the marine sampling environment, parameter estimates were highly dependent on relatively rare, high values. In small samples these extreme observations can dominate parameter estimates; on the other hand, their absence can lead to severe underestimates of the mean and variance. The dependence of these parameter estimates on the maximum observed value is shown in Figure 3 for the case $k = 0.2$, $n = 50$.

Overestimating the variance (and concomitantly, the mean) produces wide confidence intervals which, though imprecise, tend to be accurate in that they include the population mean. Conversely, underestimating the variance often leads to confidence intervals that are too small and exclude the true mean. These trends account in principle for the distributions of samples producing confidence limits that were too low or too high (Table 2). For the same reason that the "curves" in Figure 2 are not smooth, the numbers in Table 2 yield only approximate probabilities, but these should serve as useful indicators of the effects of sample size and contagion on measuring precision.

TABLE 1

Summary Statistics of Sample Means from Negative Binomial "Populations" of 50,000 Numbers with $\mu = 10$ and Parameter k as Indicated

	n	m	LL	UL	w	$4\mu(kn)^{-1/2}$	$\frac{UL - \mu}{\mu - LL}$
$k = .1$	20	9.9	1.15	26.25	25.1	28.3	1.84
	50	10.3	3.44	20.92	17.5	17.9	1.66
	100	9.9	4.90	16.66	11.8	12.6	1.31
	200	9.9	6.06	14.67	8.6	8.9	1.19
	500	10.0	7.51	13.07	5.6	5.7	1.23
	1000	10.0	8.06	12.01	4.0	4.0	1.04
$k = .2$	20	9.9	2.70	21.70	19.0	20.0	1.60
	50	9.9	4.72	16.64	11.9	12.6	1.26
	100	10.0	6.10	14.89	8.8	8.9	1.25
	200	10.0	7.075	13.475	6.4	6.3	1.19
	500	10.0	8.07	12.01	3.9	4.0	1.04
	1000	10.0	8.66	11.37	2.7	2.8	1.02
$k = .4$	20	9.9	4.05	18.70	14.65	14.1	1.46
	50	10.0	6.00	14.78	8.8	8.9	1.20
	100	9.9	7.02	13.10	6.1	6.3	1.19
	200	10.0	7.87	12.265	4.8	4.5	1.06
	500	10.0	8.58	11.56	3.0	2.8	1.10
	1000	10.0	9.01	11.03	2.0	2.0	1.04

LL = 2.5th percentile; UL = 97.5th percentile; w = UL − LL; n = sample size; m = average of sample means.

Ideally, 95% confidence limits should be higher than the true mean 2.5% of the time and lower

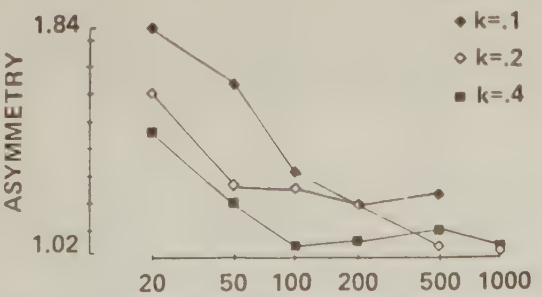

Figure 2. Asymmetry (see Table 1) of the distribution of sample means as a function of sample size (n) for three levels of contagion, k

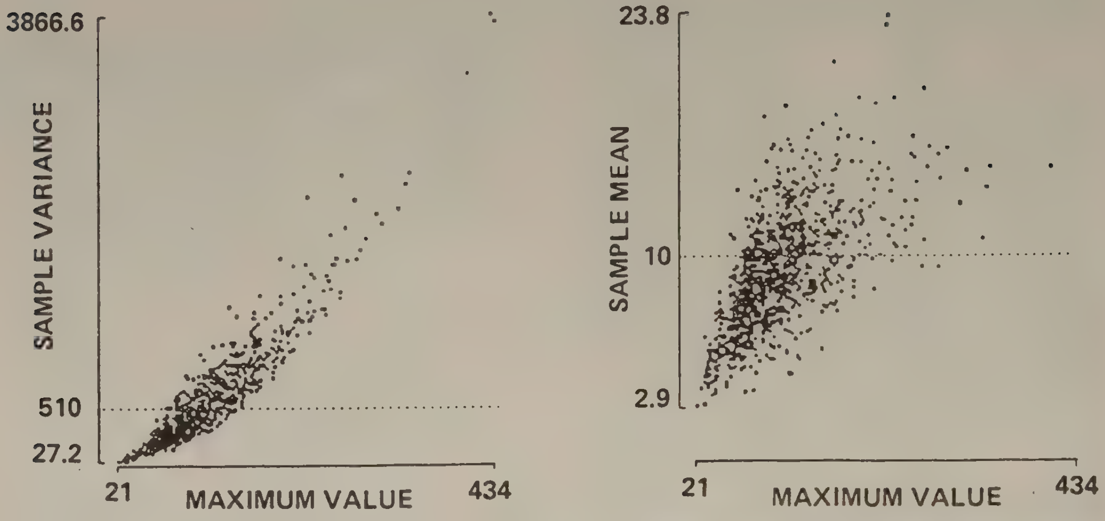

Figure 3. Dependence of estimates of the variance and mean on maximum observed value. All samples were of $n = 50$ from a negative binomial population with mean = 10, variance = 510 (k = .2).

TABLE 2
Summary of Samples (from 1000 Iterations) Giving Computed 95% Confidence Limits (CL) That Excluded the Population Mean (μ).

	k	$n=20$		$n=50$		$n=100$		$n=200$		$n=500$		$n=1000$	
		L	H	L	H	L	H	L	H	L	H	L	H
Formula 1	.1	249	1	151	3	110	1	86	4	60	7	50	5
	.2	188	4	119	5	71	3	57	6	59	9	34	12
	.4	144	4	82	8	62	3	50	7	37	20	33	16
Formula 2	.1	162	22	90	22	66	14	54	14	42	15	36	20
	.2	117	26	66	19	42	23	35	27	42	21	30	18
	.4	89	25	50	19	41	11	38	22	29	28	28	22

Formula 1: $m \pm t_\alpha \cdot \mathrm{SE}$

Formula 2: $m \cdot \exp\{\pm t_\alpha \sqrt{[\ln(1 + \mathrm{SE}^2/m^2)]}\}$
where t_α was approximated as = 2.

L = number of upper CL's that were lower than μ; H = number of lower CL's higher than μ.

than the mean 2.5% of the time; i.e., the "tails" should be equal and add to 5%. For the simulations presented here (1,000 samples each), the tails should each average 25 samples. As shown in Table 2, the low tail (L) was always > 25, and the high tail (H) usually < 25. The log-based method (formula 2) was superior to the conventional symmetrical limits (formula 1), but approached equal tails only at high n ($\geq$ 500) and k (.4). Because the simulated values of k are realistic, and larger values of n are often not, it is desirable to find a method that will further increase the asymmetry (shorten the low tail and lengthen the high) of computed confidence intervals. One promising approach is applied to real data, below.

Real Data

The three "populations" of real anchovy-egg data (summarized in Table 3) were all positively skewed and peaked (leptokurtic), with large differences between mean and median values. In all cases the variance exceeded the mean squared, implying a high degree of contagion with values of the negative binomial parameter $k < 1$. For various reasons, including the truncation of zeros and the composite nature of the data sets (amalgamation of several years' sampling), the negative binomial distribution is only an approximate model for these

TABLE 3
Characteristics of Three Populations of Anchovy Egg Data Compiled from 2,311 Positive CalVET Tows from 6 Surveys, 1980–85

Population	Mean	Median	Maximum	s^2	Skewness	Kurtosis	k	Freq(0)
A	9.88	2	261	426	5.36	42.45	.343	678
B	7.93	2	468	296	10.84	235.32	.394	632
T	24.22	10	605	1448	4.34	35.92	.656	0

A, B = first and second whole days after spawning, T = total eggs.

populations. This can be verified, for instance, by comparing the maximum likelihood estimates of k (Table 3) with the asymptotic moments relationship, $k' = m^2/(s^2 - m)$. However, as will be seen below, small samples from these distributions will tend to be negative-binomial-like enough that the null hypothesis in goodness-of-fit tests will seldom be rejected.

Ten random samples at each of five sample sizes (20 to 500, Table 4) were drawn from each of the three populations. At sample sizes < 500, the sample mean bore an approximately linear relationship to the maximum observations, shown for the A samples in Figure 4. Only one T sample (#7 at $n = 20$) produced a confidence interval that excluded the mean, but 16% of samples from the more positively skewed A and B populations (which also had $> 25\%$ zeros, Table 3) at $n \leq 200$ produced estimates of the mean that were more than 2 standard errors below the true value. The

TABLE 4

Mean (m), Median (md), Maximum (max), and Standard Error (SE) of Samples of *Engraulis mordax* Eggs

	m	md	max	SE		m	md	max	SE		m	md	max	SE
A20	11.25	1	71	4.57	B20	4.55	1	27	1.59	T20	19.30	8	127	6.85
	11.85	3	71	4.09		4.25	1	47	2.33		15.55	7	83	4.31
	10.30	4	48	3.43		4.00	2	15	0.99		29.10	17.5	173	8.63
	7.25	1	37	2.67		7.05	1	34	2.22		24.95	9.5	144	8.09
	7.90	4.5	39	2.29		9.80	1.5	38	2.98		19.00	3	177	10.81
	7.45	3.5	47	2.89		9.95	5.5	61	3.32		25.10	15	114	6.55
	10.80	5	46	3.17		11.05	3	46	3.41		11.45	6	61	3.12
	10.30	7	39	2.35		6.70	1	34	2.40		46.70	19	252	14.58
	9.65	1.5	79	4.35		8.45	3	36	2.42		18.45	13.5	60	3.97
	7.10	1	55	3.31		3.75	1	27	1.44		23.40	11	106	7.14
A46	10.30	1	99	3.16	B46	10.09	3	86	2.57	T46	31.89	15	201	6.10
	5.80	1	71	1.86		4.44	1	37	1.20		21.52	11.5	97	3.84
	4.85	2	26	1.01		9.13	2.5	74	2.36		32.13	16	166	6.20
	12.15	6	71	2.57		15.91	2.5	468	10.15		25.54	8.5	140	4.91
	17.54	3	247	6.52		8.17	1	55	2.00		25.67	14.5	242	6.06
	11.35	4	94	2.53		10.74	3	119	3.03		19.96	8.5	117	3.65
	10.67	3	127	3.25		10.59	2	142	3.62		20.63	9.5	167	5.17
	7.96	3	109	2.54		7.78	1.5	88	2.23		30.67	15.5	177	6.07
	5.35	1.5	53	1.37		10.48	2.5	83	2.77		31.13	19	157	5.49
	10.80	3.5	84	2.78		6.37	2.5	35	1.28		28.94	16	248	6.27
A100	10.20	2	102	1.91	B100	8.19	2	128	1.73	T100	22.35	6.5	174	3.59
	9.38	3	119	1.69		5.71	2	39	0.88		24.04	13	147	2.92
	11.83	3	170	2.42		6.15	3	45	0.83		29.03	12	342	5.08
	11.93	3	244	2.94		12.35	1	468	4.94		25.27	7	382	4.70
	10.44	3	201	2.45		8.94	3	87	1.63		21.66	7.5	168	3.35
	7.46	2	87	1.38		10.71	3	201	2.61		24.34	9	217	3.82
	13.50	2	229	3.22		5.85	2	59	0.94		23.43	8.5	252	3.59
	9.54	3	118	1.76		14.15	3	468	4.89		22.52	11	171	2.83
	10.69	4.5	170	2.02		10.24	2.5	201	2.64		21.27	11	273	3.47
	10.12	4	65	1.35		6.86	2	69	1.15		27.46	10.5	173	3.80
A200	9.80	2	126	1.34	B200	8.60	3	131	1.10	T200	26.72	10.5	605	3.86
	12.28	3	245	1.88		7.95	1.5	142	1.20		22.05	9	174	2.22
	11.35	3	157	1.47		7.41	3	119	0.94		22.11	7	168	2.24
	13.43	3	261	2.12		9.94	4	140	1.24		22.49	9	273	2.42
	7.52	3	64	0.78		7.29	2	131	1.09		21.27	9	174	2.09
	9.26	3.5	157	1.28		5.98	2	42	0.60		25.77	9	273	2.82
	10.15	3	157	1.40		7.71	2	88	1.00		21.25	7	217	2.40
	7.96	2	94	1.05		7.23	3	64	0.81		23.05	10	252	2.42
	9.52	3	132	1.27		7.65	2	75	0.92		23.61	8	211	2.46
	10.59	2.5	261	1.69		7.62	2	142	1.08		21.33	10	195	2.06
A500	9.48	2	229	0.95	B500	7.79	3	420	0.61	T500	23.52	10.5	249	1.49
	9.52	2	229	0.91		8.49	2	468	1.13		24.26	9	251	1.70
	10.10	2	261	0.97		7.89	2	142	0.66		23.16	10	342	1.60
	10.40	3	261	0.97		8.49	2	128	0.67		22.20	10	342	1.45
	10.28	2	245	1.03		8.31	2	201	0.72		21.36	9	382	1.55
	8.88	2	245	0.83		8.19	3	140	0.64		26.23	11	605	2.06
	10.79	3	170	0.95		9.81	2	468	1.23		22.11	9	215	1.39
	10.82	3	261	1.04		8.11	3	201	0.68		23.51	10	251	1.54
	11.38	3	247	1.18		8.15	2	468	1.15		24.90	9	605	1.96
	10.66	3	201	0.98		7.86	2	142	0.67		23.35	11	342	1.59

A = first whole day, B = second whole day after spawning; T = total eggs. Number after age designation is sample size.

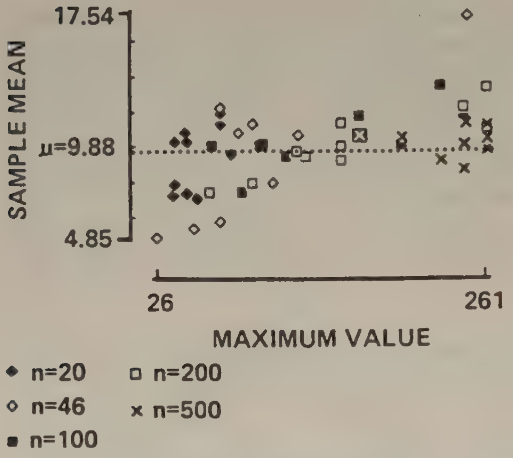

Figure 4. Dependence of the sample mean on the maximum observed value of samples drawn from a "population" of northern anchovy eggs (population A, Table 3).

worst case was sample A46#3, with sample mean = 4.85 and standard error = 1.01. The 95% confidence limits by formula 2 for this sample are 3.2–7.3, well below the true mean value of 9.9. However, the adaptation of Easterling's "consonance region" produced an interval estimate for the mean (3.5–10.5) that included the true value (Table 5). This method thus shows promise of reducing the frequency of samples in the "low tail," found above to be several times too high at sample sizes < 500.

At the other extreme among A samples was A46#5, with mean = 17.54 and standard error = 6.52. The high mean and variance of this small sample were strongly affected by the maximum value of 247 (Table 4; Figure 4), giving a wide confidence interval by formula 2 of 8.54–36.02. The consonance region for this sample gives credence to a narrower range of values for the population mean (approximately 7–14, Table 6), excluding the sample mean but still containing values above and below 9.9, the true mean. The effect of the very high maximum value on estimates of central tendency and dispersion was therefore moderated by the shape of the rest of the data in the sample. Besides the maximum value, sample A46#5 also chanced to have two other values > 100 but a median of only 3, characteristics that contribute to the bilobed nature of the consonance region as computed here.

The goodness-of-fit results of Table 6 also suggest that the negative binomial may be a poor general model for the data of sample A46#5, as no *p* ⩾ .5 region was found. If these data were all that we knew about the population, with what confidence could we make statements about its parameters? Before such questions can be answered, work must be done to quantify the distribution of consonance regions for contagiously distributed data, and to work out the robustness of the method to departures from completely specified distribution

TABLE 5

Chi-Square Probabilities of Goodness of Fit to Sample A46 #3 (See Table 4) of Negative Binomial Models with Parameters *m* and *k*

m	*k*														
	.2		.3		.4		.5		.6		.7		.8		.9
12.5			.1												
12.0			.1	.1											
11.5			.1	.1	.1										
11.0			.1	.1	.1										
10.5			.2	.2	.1	.1									
10.0			.2	.2	.2	.1		.1							
9.5			.1	.2	.2	.2	.2	.1							
9.0			.2	.2	.2	.2	.2	.2	.1						
8.5			.2	.2	.2	.2	.2	.1							
8.0			.2	.2	.5	.2	.2	.2	.1	.1					
7.5			2	.2	.5	.5	.2	2	.1	.1					
7.0			2	.2	.5	.5	.5	.2	.2	.2	.1				
6.5			.2	.2	.5	.5	.5	.2	.2	.2	.2	.1			
6.0		.1	.2	.2	.5	.5	.5	.5	.2	.2	.2	.1			
5.5		.1	.2	.5	.5	.5	.5	.5	.5	.2	.2	.1			
5.0		.1	.2	.5	.5	.5	.5	.5	.5	.2	.2	.2	.2	.1	.1
4.5		.1	.2	.5	.5	.5	.5	.5	.2	.2	.5	.2	.2	.2	.1
4.0			.2	2	.5	.5	.5	.2	.5	.2	.1	.1		.2	.1
3.5			.1	.2	.1	.2	.2	.2	.2	.2	.2	.1	.1		
3.0					.1	.1			.1	.1	.1				

TABLE 6

Chi-Square Probabilities of Goodness of Fit to Sample A46 #5 of Negative Binomial Models with Parameters *m* and *k*

m	*k*										
	.25		.35		.45		.55		.65		.75
15.0			.1								
14.5			.1								
14.0		.2	.1								
13.5		.2	.1								
13.0		.2	.1								
12.5		.2	.1								
12.0		.2	.1								
11.5		.2	.1								
11.0		.2	.1								
10.5		.1	.1	.1							
10.0		.1	.1								
9.5		.2	.1				.1				
9.0		.1	.1		.2	.1					
8.5		.1		.2	.2						
8.0		.1	.2	.2	.2				.1	.1	
7.5		.1		.2	2	.2	.2	.1	.1		.1
7.0			.1	.2	.2	.1	.1	.1	.1		
6.5					.1	.1	.1				
6.0											

models. Because of the astronomical number of computations required, it is very unlikely that generally applicable tables will be forthcoming. However, solutions to specific situations, with a few models over a limited range of parameters, should be producible for a given research application.

One obvious limitation of the consonance region approach is that as sample size increases, the statistical power to reject the null hypothesis (i.e., no difference between sample and specified frequency distribution) increases as well. The consonance region will become correspondingly small until some practical limit is reached. At such a point it may be plausible to use models with more parameters, as suggested by Easterling (1976), but as sample size increases, so does the suitability of simpler fiducial methods, such as formula 2.

When, as in pelagic fish-egg and larval census work, the potential exists for a few observations to dominate parameter estimates, the best insurance against wrong estimates is large sample size. In some applications, the costs of increasing sample size may seem too high, and the lower precision of small samples may be acceptable. We have emphasized here that special methods are needed in these cases in order to make correct probability statements about the population. We are not advocating the use of small samples. Rather, it is hoped that the above examples and the data of Table 2 will be helpful to planners who must weigh the costs and benefits of various approaches to sampling contagiously distributed organisms.

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Status of early life history studies of northeast Pacific rockfishes

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Abstract

Rockfishes (Sebastes spp.) are highly unusual in that they have internal fertilization of a large number of eggs (>10^5) and give birth to planktonic larvae at the first feeding stage. Following the planktonic larval stage, juveniles develop in a variety of habitats, depending on the species. Some remain pelagic for several months, while others become demersal at a small size. Since about 70 species of rockfish occur in the northeast Pacific, identifying the larvae and juveniles is a major problem. Recent studies have greatly enhanced our ability to identify these young stages, which allows us to contemplate using them to address fishery-related problems. Current studies are focused on relating the abundance of larvae and juveniles of rockfish to the adult populations, to measure both adult biomass and recruitment. These studies show promise, but the unusual biology of the genus limits somewhat the potential of such studies for fishery management purposes.

Early Life History Pattern

Rockfishes have an unusual reproductive pattern with important implications for their ecology and fisheries on their populations. Most fish that reproduce in marine waters lay free-floating planktonic eggs that are fertilized and undergo embryonic development as independent organisms in the open sea. Hatching is followed by a yolk-sac period about one-half as long as incubation, during which the larva develops eye pigment and feeding mechanisms. In rockfishes, however, fertilization occurs internally and the eggs develop and hatch inside the ovary of the female. It has recently been found that the embryos ingest ovarian fluid as a supplement to the yolk (see Boehlert, Kusakari, and Yamada, this volume). When the larvae are extruded after several weeks, they have little yolk left and are ready to begin feeding. These larvae are about 3-7 mm standard length (SL), comparable in size to first-feeding larvae of species with planktonic eggs.

Mortality of planktonic fish eggs, due primarily to predation, is high for the few species that have been studied in enough detail to make reliable estimates. Generally more than 50% of the pelagic eggs spawned by a fish die before hatching (Hempel 1979). Mortality of yolk-sac larvae in the field is even more difficult to examine but predators that feed on eggs probably also consume yolk-sac larvae. Thus, less than 20% of eggs spawned may survive through the yolk-sac period to become free-feeding larvae. Boehlert et al. (this volume) estimate that there is about 25% mortality of young in rockfishes between fertilization and parturition. Thus, the number of surviving first-feeding larvae in rockfishes is about 75% of the number of eggs that undergo ovulation, rather the 20% or less of that number in fishes spawning pelagic eggs. Also, the reproductive pattern of rockfishes reduces the amount of dispersion of planktonic stages by ocean currents.

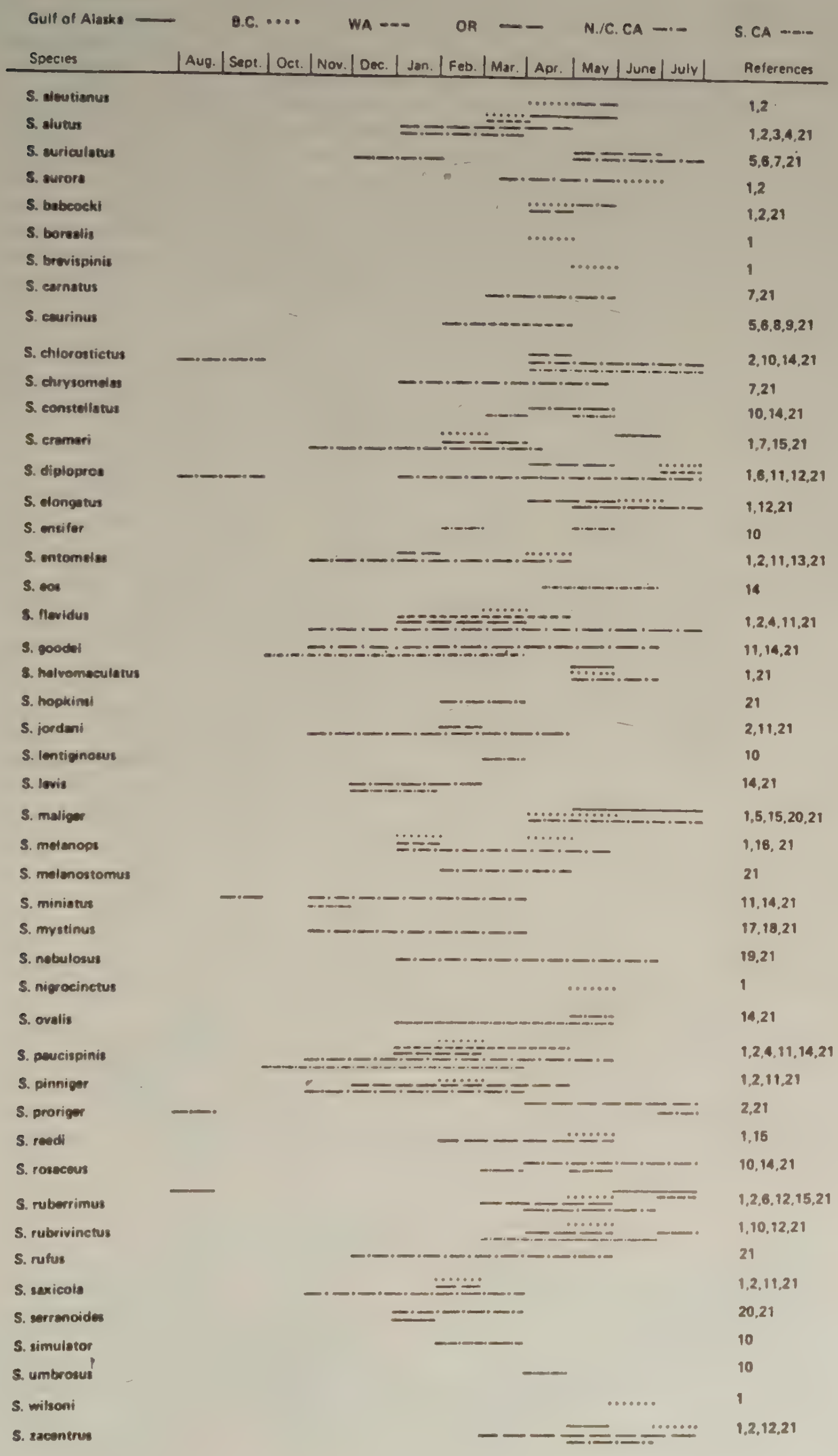
Fecundity of rockfishes is high (10^4-10^6 eggs per female) and is only slightly lower than it is in fishes spawning pelagic eggs. In fish with more extensive protection of the young, or those that produce considerably larger eggs, fecundity is reduced substantially. It would seem that rockfishes have not achieved the concomitant reduction in fecundity generally associated with increased parental contribution to the welfare of individual progeny. The evolutionary advantage of gestation in rockfishes is unclear, but apparently it is not completely explained by protection of the egg and early larval stages. Internal fertilization may allow distinct but similar species to co-occur with little chance of cross-fertilizing their gametes. Behavioral or other prezygotic barriers would prevent copulation among closely related species. This reproductive strategy may have contributed to the genus becoming so speciose in the North Pacific.

Seasonality of Reproduction

Reproductive events in rockfishes follow this sequence: spermatogenesis, vitellogenesis, mating, ovulation, fertilization, embryonic development, hatching, and larval extrusion. Males mature up to several months before the females, and mating may precede fertilization by several months. Embryonic development takes about 40-50 days, and the larvae hatch about 1 week prior to extrusion. Although most rockfishes release larvae during the first 6 months of the year, there is quite a bit of variation among the species, and within a species among years.

When comparing information on seasonality of reproduction, the methods and criteria used and the sample sizes must be evaluated. Most work to date has been done off British Columbia and north/central California. Wyllie Echeverria (in press) has summarized information on reproductive seasonality of 34 species of northeast Pacific rockfish. The duration of larval release varies from 1 to 9 months among the species studied, and a few species demonstrated two periods of release during the year (Table 1). In general, species can be grouped into those that extrude larvae in winter and those that extrude larvae in spring-summer.

Table 1.--Periods of release of rockfish larvae. Based on Wyllie Echeverria (in press).



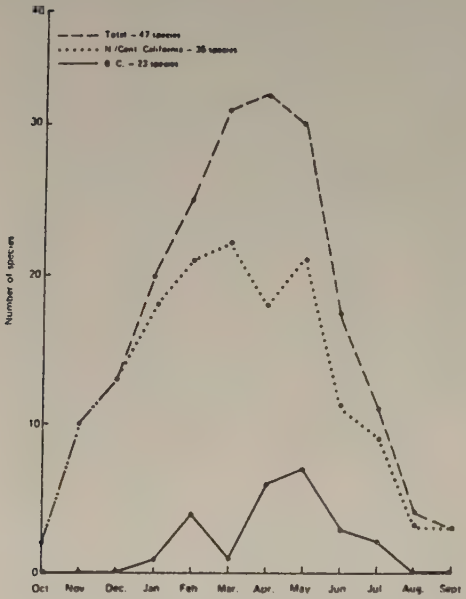


Figure 1.--Number of rockfish species releasing larvae off north / central California and British Columbia by month. Based on Wyllie Echeverria (in press).

Parturition seems to occur earlier in the year in the southern part of the species' range, although data sufficient for such a comparison is available for few species. Annual differences in timing of release of larvae seem to be environmentally determined. In some species studied by Wyllie Echeverria (in press), parturition during the anomalous El Nino year of 1983 was delayed compared to the other years from 1981 to 1985.

Summarizing the data presented by Wyllie Echeverria (in press), there seems to be a slight tendency for rockfishes in the north (British Columbia) to release young later in the year (April-June) than those off north/central California which release young mainly from January to May (Fig. 1). Also, a longer period of release is apparent off north/central California than off British Columbia (Table 2). The median period of release off British Columbia is 1 month, whereas off north/central California it is 3 months. These differences could partially be due to differences in sampling density.

Table 2.--Duration of parturition period of rockfishes by area and number of species (based on Wyllie Echeverria, in press).

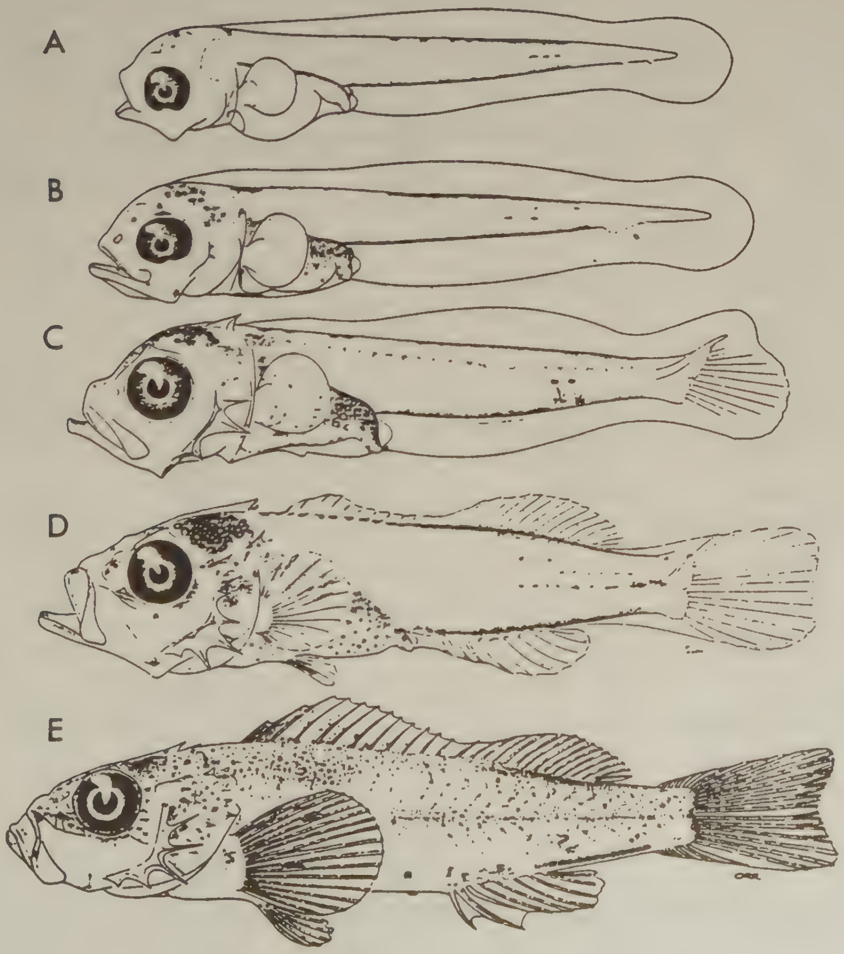
	Area					
Number of months	G of A	BC	Wa	Or	N/C Ca	S Ca
	-----------------	----------------	number of species	----------------	----------------	----------------
1	3	21	2	6	3	2
2	1	2	1	6	5	5
3	2		2	1	8	1
4				4	2	2
5				2	7	1
6					5	2
>6					5	
total	6	23	5	19	35	13*

*3 species have split season with no release in March or April.

Larval Development

Rockfish larvae are about 3-7 mm SL at birth and have pigmented eyes and a functional mouth (Fig. 2). The trunk and tail is surrounded by an undifferentiated finfold and larval pectoral fins are present. Pigment generally consists of small discrete melanophores in characteristic positions. Although there is considerable interspecific variation in melanophore amount and placement, from nearly absent in S. helvomaculatus to a dark banded pattern on the body of S. aurora, In almost all species some pigment is found on the gut and there is usually a series of postanal ventral midline melanophores. Depending on the species, melanophores may also occur on such places as the jaws, top of head, nape, pectoral fins, dorsal postanal midline, or midlaterally on the caudal peduncle and near the tip of the notochord. Superficial pigment is added in definitive patterns as the juvenile period is approached.

Figure 2.--Development of Sebastes dalli (from Moser and Butler 1981). A. 5.1 mm larva; B. 6.2 mm larva; C. 7.1 mm larva; D. 10.1 mm larva; E. 21.7 mm pelagic juvenile.



With development, the body deepens somewhat and the head enlarges. In postflexion larvae head length is about 28-48% of the body length, preanal length is about 42-66% of the body length, and the maximum body depth is about 21-42% of the body length (Table 3). Head spines start to develop early in the larval period, and soon reach their maximum number and relative size. A full or nearly full complement of spines develops during the larval period, but some are usually lost during the juvenile period to produce the adult pattern that is a specific character. The first head spines to form are the pterotics, several of the preoperculars, and the parietals. Spines continue to be added and to increase in size as the larvae develop. The parietal spines, some of the preopercular spines, and the supraocular ridge become serrate in some species. The parietals and central preoperculars are the longest spines, the parietals reaching 27% of the head length in *S. helvomaculatus* (Richardson and Laroche 1979). Fin ray formation follows this sequence: caudal, pectorals, pelvics, dorsal, and anal. Fin rays are generally not particularly elongate, although there is variation in the length of the pectoral rays with *S. paucispinis* pectorals reaching 37% body length in postflexion larvae (Moser et al. 1977). Pelvic rays develop uniquely early in 5-mm larvae of *S. paucispinis*, and reach the same elongate proportion as the pectorals.

Table 3.--Morphometric characters of postflexion larvae of 16 species of northeast Pacific rockfishes, expressed as ranges of percent standard length (SL).

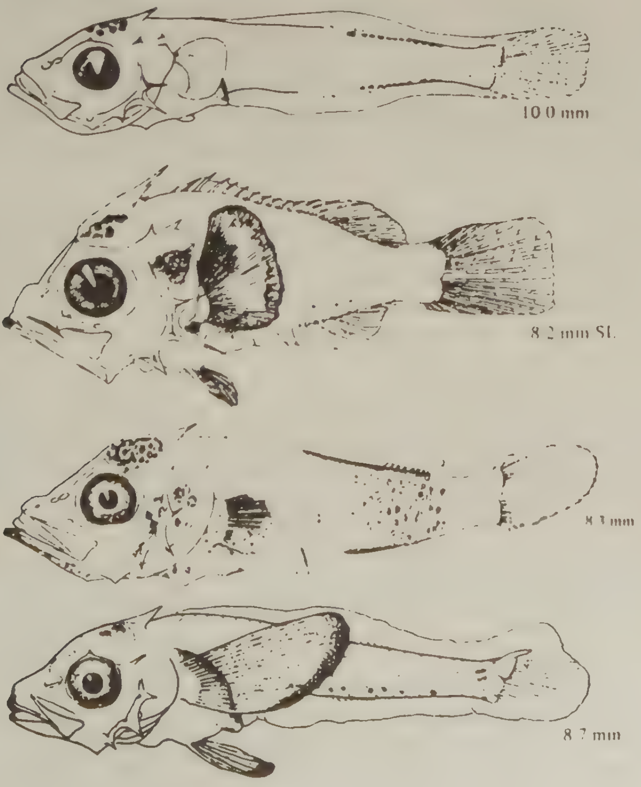
Species	Head length	Body depth	Preanal length	References*
S. auriculatus	30 - 38	22 - 29	47 - 53	20
S. aurora	33 - 40	26 - 34	56 - 66	18
S. caurinus	29 - 36	21 - 29	42 - 54	20
S. crameri	37 - 43	30 - 35	55 - 65	19
S. dalli	28 - 33	22 - 28	48 - 56	16
S. entomelas	34 - 39	25 - 30	55 - 61	9
S. flavidus	35 - 43	25 - 31	54 - 61	8
S. helvomaculatus	40 - 44	33 - 34	59 - 60	19
S. jordani	31 - 36	22 - 26	46 - 54	15
S. levis	34 - 38	33 - 36	57 - 63	15
S. macdonaldi	34 - 41	33 - 36	55 - 64	15
S. melanops	35 - 43	26 - 33	54 - 62	8
S. melanostomus	39 - 44	37 - 42	55 - 63	14
S. paucispinis	36 - 39	28 - 31	51 - 61	15
S. pinniger	38 - 48	34 - 42	52 - 63	19
S. zacentrus	40 - 46	33 - 36	54 - 62	9

*Numbers key to references in Literature Cited.

Larval Identification

Two approaches, or a combination of both, are used to establish the identity of larval fish. The direct approach involves rearing larvae from known parents. The indirect, or series approach, involves finding specimens in field samples that are large enough to have definitive adult (mainly meristic) characters, but small enough to retain some larval characters (such as pigment). A series of similar looking but smaller specimens is accumulated from field samples until the smallest larvae can be recognized. With northeast Pacific rockfishes, yolk-bearing larvae of 50 species have been reared, but only seven species have been reared to caudal fin formation, and only one species has been reared through the larval period. The caudal fin formation larvae are helpful, but not completely definitive, in establishing the identity of field-caught specimens, and the yolk-bearing larvae offer little help at the level to which they have been studied. Thus, with rockfishes larval identification has depended mainly on establishing series. A few species such as *S. jordani*, *S. paucispinis*, *S. aurora*, and *S. melanostomus* have proven to have very distinctive larvae at all stages of development (Fig. 3) but most, particularly before notochord flexion, seem to look very similar. In several descriptions based on the series approach, larvae smaller than 8-10 mm SL could not be recognized with confidence.

Figure 3.--Flexion stage larvae of (top to bottom) *S. jordani* (from Moser et al. 1977), *S. melanostomus* (from Moser and Ahlstrom 1978), *S. aurora* (from Moser et al. 1985), and *S. paucispinis* (from Moser et al. 1977).



Descriptions of larvae and pelagic juveniles of various rockfishes are slowly accumulating in the literature, making it reasonable to contemplate using the planktonic stages in field samples for fisheries studies. Among northeast Pacific rockfishes, illustrations have been produced for yolk-sac or preflexion larvae of 50 species, complete larval series of 8 species, and pelagic juveniles of 39 species (Table 4).

Table 4.--Key to sources of illustrations of rockfish larvae from the northeast Pacific Ocean. Numbers key to references in Literature Cited.

Area of occurrence	Larval Stage					Juvenile Stage	
Species	Yolk sac	Preflexion	Flexion	Postflexion	Transformation	Pelagic	Benthic
West Coast of North America							
S. *aleutianus*	4, 24					7	7
S. *alutus*	3, 4, 24					7	7
S. *atrovirens*							
S. *auriculatus*	3, 15, 20	20	20	7		7	7
S. *aurora*		18	18	18	18	18	18
S. *babcocki*	3, 4, 24			7		7	7
S. *borealis*							7
S. *brevispinis*	3, 4, 10					7	
S. *carnatus*	12, 15						
S. *caurinus*	3, 10, 15, 20	20	20	7		7	7
S. *chlorostictus*	12, 15			7	7	7	7
S. *chrysomelas*							
S. *ciliatus*	6						
S. *constellatus*	12, 15, 17		17	17			
S. *crameri*	24			19	19	7, 19	7, 19
S. *dalli*	12, 15, 16	16	16	16		16	
S. *diploproa*	3, 25			7		7	7
S. *elongatus*	12, 15, 25			7		7	7
S. *emphaeus*				7		7	7
S. *ensifer*	12, 15						
S. *entomelas*	6, 17			9	9	7, 9	7, 9
S. *eos*	12, 15						
S. *flavidus*	3			8	8	7, 8	7, 8
S. *gilli*	15						
S. *glaucus*							
S. *goodei*	11, 15					7	
S. *helvomaculatus*	25			19	19	7, 19	7
S. *hopkinsi*	12, 15						
S. *jordani*	10, 11	2, 15		2, 15	2, 15	2, 7, 15	7
S. *lentiginosus*							
S. *levis*	2, 12, 15		2, 15	2, 15	2, 15	2, 15	
S. *macdonaldi*	2, 12, 13, 15	2, 13, 15	13	2, 13, 15	2, 13, 15	2, 13, 15	13
S. *maliger*	3, 25			7	7	7	7
S. *melanops*	10			8	8	8	7, 8
S. *melanosema*							
S. *melanostictus*							
S. *melanostomus*	14, 15			14	14	14	7, 14
S. *miniatus*	15					7	7
S. *mystinus*	4, 22			7		7	7
S. *nebulosus*							7
S. *nigrocinctus*						7	7
S. *notius*							
S. *ovalis*	12, 15, 17	17					
S. *paucispinis*	2, 11, 12, 15	1, 2, 12, 15	1, 2, 12, 15	1, 2, 12, 15	2, 12, 15	7, 12	7
S. *phillipsi*							
S. *pinniger*	15, 21			19	19	7, 19	7, 19
S. *polyspinis*	10					7	
S. *proriger*	25			7		7	7
S. *rastrelliger*						7	7
S. *reedi*	24					7	7
S. *rosaceus*	12, 15					7	7
S. *rosenblatti*	15						
S. *ruberrimus*	3, 5, 6, 25					7	7
S. *rubrivinctus*	17						
S. *rufinanus*							
S. *rufus*	15, 17	17	17				
S. *saxicola*	11, 24			7		7	7
S. *semicinctus*	12, 15						
S. *serranoides*	17	17					
S. *serriceps*	15						
S. *simulator*							
S. *umbrosus*	12, 15						
S. *variegatus*	6, 10			7			7
S. *wilsoni*				7		7	7
S. *zacentrus*	4, 6, 10, 25			9	9	7, 9	7, 9
Gulf of California endemics							
S. *cortezi*	15	15		15		15	
S. *exsul*							
S. *peduncularis*							
S. *sinensis*							
S. *spinorbis*							
S. *varispinis*							

Westrheim (1975) concluded, based on work with preextrusion larvae of 31 species, that "interspecies similarities and intraspecies differences in morphometric and meristic characteristics of preextrusion Sebastes larvae delineated in this study clearly preclude accurate identification, based only on these criteria, of Sebastes larvae caught at sea." He also found that larvae of several species reared to yolk exhaustion changed significantly in pigment pattern from preextrusion larvae. The yolk-sac period in most fishes is characterized by changes in pigment pattern as embryonic pigment migrates and is increased to form the larval pigment pattern. The larval pigment pattern is still not well established in yolk-exhaustion rockfish larvae, so it does not appear possible to anticipate what more advanced plankton-caught larvae of a particular species will look like based on pigment observed in reared preextrusion or yolk-exhaustion larvae.

In spite of these problems there are indications that more detailed studies of reared yolk-sac larvae of rockfishes may be helpful for identifying field-caught specimens. Examining the published illustrations of yolk-sac larvae of 46 species of rockfishes, we established 26 loci where pigment was observed (Fig. 4). We then scored each species based on the presence or absence of pigment at these loci. We found that only two pairs of species could not be separated on the basis of this pigment criterion. There may be problems in comparability of the illustrations because of different illustrators, intraspecific pigment variations, different stages of development, and uncertainty with some adult identifications. However, this excercise indicates that there indeed may be enough interspecific difference in pigment to warrant further study.

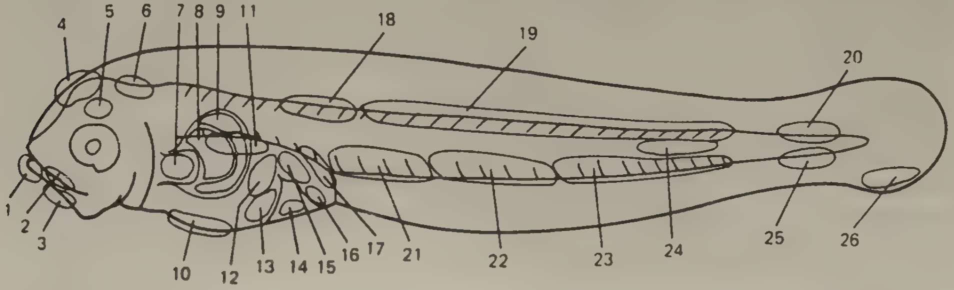
Also, we noted, in the published illustrations and on specimens of several species at our disposal, considerable variation in the appearance of the melanophores that are present on or near the hindgut. The number, size, and location of these seem to be rather consistent within a species, and there is considerable variation among species. Further study will be required to test the utility of this pigment for species separation.

While some changes in pigment occur between hatching and yolk exhaustion, we were struck in the several series we examined by the consistency of pigment in some areas. This indicated that the problem of comparing illustrations and descriptions of preextrusion and yolk-exhaustion larvae may not be severe enough to negate their value completely.

Besides pigment, yolk-bearing larvae have other characters that may be profitable to evaluate. Morphometric characters such as size at stage of development, body depth, and preanal length may prove important. All of the illustrations summarized by Westrheim (1975) were produced by sketching pigment onto a basic template drawing of a rockfish yolk-sac larva. Thus, no morphometric comparisons can be made of these illustrations. Further, the pectoral fins were not included on these illustrations, so the pigment characters of the pectoral fin can not be evaluated for these larvae.

Western Pacific rockfishes, which are larger at extrusion than those in the eastern Pacific, have been reared in large numbers through the juvenile stage for release to enhance natural production (see Moser and

Figure 4.--Pigment loci on yolk-sac larvae of rockfishes. In the body of the table, "1" means pigment present, "2" means pigment absent.



Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
	Pigment Loci																									
S. entomelas	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1	2	2	1	1	1
S. ciliatus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	2	2	1	2	1	2	2	1	2	1
S. crameri	1	1	1	1	1	1	1	1	1	1	1	2	2	1	2	2	2	1	1	1	1	2	2	1	2	1
S. mystinus	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	2	1	1	1	1	2	2	1	1	1
S. alutus	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	2	1	1	1	1	2	2	1	1	1
S. semicinctus	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	2	1	2	1	2	2	2	1	1	1
S. rubberrimus	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	2	1	1	1	1	2	2	1	2	1
S. hopkinsi	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	2	1	2	1	1	2	2	1	1	1
S. variyatus	1	1	1	1	1	1	1	1	1	1	2	1	1	2	1	2	2	1	1	1	1	2	2	1	2	1
S. brevispinis	1	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1	2	1	1	1	1	2	2	1	2	1
S. reedi	1	1	1	1	1	1	1	1	1	1	2	2	1	1	2	1	2	1	1	1	1	2	2	1	2	1
S. aleutianus	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	1	1	2	1	2	2	1	2	2
S. helvomaculatus	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	2	1	1	1	1	2	2	1	1	1
S. carnatus	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1	1	2	1	2	1	2	2	2	1	1	1
S. flavidus	1	1	1	1	1	1	1	1	1	2	2	1	1	1	1	2	2	1	1	1	1	2	2	1	2	1
S. zacentrus	1	1	1	1	1	1	1	1	1	2	2	2	2	1	1	2	2	1	2	2	1	2	2	2	2	2
S. paucispinus	1	1	1	1	1	1	1	2	2	1	2	1	1	1	1	2	2	1	1	1	1	2	2	1	1	1
S. rosaceus	1	1	1	1	1	1	1	2	2	2	2	1	1	2	1	1	2	1	1	1	2	2	2	1	1	1
S. cortezi	1	1	1	1	1	1	2	2	1	2	2	1	1	1	2	1	2	1	1	1	1	2	2	1	2	1
S. rufus	1	1	1	1	1	2	1	1	1	1	2	1	1	1	1	1	2	1	2	1	1	1	2	1	1	1
S. saxicola	1	1	1	1	1	2	1	1	1	1	2	1	1	1	1	1	2	1	2	1	2	2	2	1	1	1
S. proriyer	1	1	1	1	1	2	1	1	1	1	2	1	1	2	2	2	2	1	1	2	1	2	2	1	2	2
S. elongatus	1	1	1	1	1	2	1	1	1	1	2	1	2	2	1	1	2	1	1	1	2	2	2	1	1	1
S. diploproa	1	1	1	1	1	2	1	1	1	2	2	1	1	1	2	2	2	1	1	1	1	2	2	1	2	1
S. babcocki	1	1	1	1	1	2	1	1	1	2	2	1	2	2	1	2	2	1	2	1	2	2	2	1	2	2
S. macdonaldi	1	1	1	1	1	2	2	2	1	1	2	1	2	2	1	1	2	1	1	1	1	2	2	1	1	1
S. jordani	1	1	1	2	1	1	1	1	1	1	2	1	1	1	2	1	2	1	2	1	1	2	2	1	1	1
S. serriceps	1	1	1	2	1	2	1	1	1	1	2	1	1	2	1	2	2	1	1	1	1	2	2	1	2	1
S. ovalis	1	1	1	2	1	2	2	1	1	1	2	1	1	1	1	2	2	1	2	1	1	2	2	1	1	1
S. goodei	1	1	1	2	1	2	2	2	2	1	2	2	2	1	2	2	2	1	1	1	1	2	2	1	1	1
S. dalli	1	1	1	2	2	2	1	1	1	1	2	1	1	1	1	2	2	1	2	1	2	2	2	2	1	1
S. gilli	1	1	1	2	2	2	2	1	1	1	2	1	1	2	2	2	2	1	2	1	1	2	2	2	2	1
S. constellatus	2	1	1	1	1	1	1	1	2	2	2	1	1	2	1	1	2	1	1	1	1	2	2	1	1	1
S. ensifer	2	1	1	1	1	1	1	1	2	2	2	1	1	2	1	1	2	1	1	1	2	2	2	1	1	1
S. pinniger	2	1	1	1	1	1	1	2	1	2	1	1	1	1	1	1	2	1	2	1	1	2	2	1	2	1
S. rosenblatti	2	1	1	1	1	1	1	2	2	2	2	1	1	2	1	2	2	1	1	1	2	2	2	1	1	1
S. eos	2	1	1	1	1	1	1	2	2	2	2	1	1	2	1	2	2	1	1	1	2	2	2	1	1	1
S. umbrosus	2	1	1	1	1	1	1	2	2	2	2	1	2	2	1	1	2	1	1	1	1	2	2	1	1	1
S. chlorostictus	2	1	1	1	1	1	1	2	2	2	2	1	2	2	1	2	2	1	1	1	2	2	2	1	1	1
S. maliyer	2	1	1	1	1	2	1	1	1	2	2	2	1	1	1	1	1	2	2	1	2	2	2	1	1	1
S. miniatus	2	1	1	2	2	2	1	1	1	1	2	2	1	1	1	2	2	1	1	1	1	2	2	1	2	1
S. caurinus	2	1	1	2	2	2	2	1	1	2	2	1	2	2	2	2	2	2	2	1	2	2	2	1	1	1
S. levis	2	1	1	2	2	2	2	2	2	1	2	1	1	1	1	2	2	1	1	1	1	2	2	1	1	1
S. auriculatus	2	1	2	2	2	2	1	1	1	2	2	1	1	1	1	2	2	2	2	1	2	2	2	1	1	1
S. melanostomus	2	2	2	1	2	2	1	2	2	2	2	2	2	1	1	1	2	1	1	1	1	2	1	1	1	1

Butler in press). However, only one eastern Pacific species (S. dalli) has been reared beyond caudal fin formation (Moser and Butler 1981). Among the other most successful eastern Pacific rearings, S. rufus lived to 46 days, S. constellatus to 38 days (Moser and Butler in press), and S. caurinus to 35 days (Stahl-Johnson 1985). Eastern Pacific rockfishes seem amenable to standard techniques developed in other marine fish, but concentrated efforts are needed to obtain healthy full-term larvae from females, and to have proper rearing conditions available for this work. Further progress in rockfish larval identification is largely dependent on rearing developmental series of a wide variety of species.

Larval Distribution

Largely because of identification problems, occurrences of rockfish larvae from ichthyoplankton surveys in the northeast Pacific are usually reported at the generic level (*Sebastes* spp.). Lisovenko (1964) discussed purported catches of *S. alutus* larvae made in the Gulf of Alaska in 1963, at a time when the population of *S. alutus* was much larger than at present. The proportion of *S. alutus* and other rockfishes in these catches is unknown, since no description of *S. alutus* is available, and Lisovenko (1964) did not provide diagnostic characters for the larvae he identified as *S. alutus*.

No field work has been designed specifically to collect rockfish larvae. Occurrences of particular species have been reported in the descriptions of the few species described from field collections (Table 5). These distributional data probably are more indicative of where sampling was conducted, and what samples were examined, than the actual distribution of the larvae. However, the larvae occur to considerable distances offshore (up to 306 km from shore), and several species were not reported nearshore (6 of the 14 species were not found closer to shore than 24 km). Most larval occurrences were in the first 6 months of the year, with the period of occurrence of 7 of the 14 species including April. The season of three species extended to August.

Table 5.--Occurrences of larvae of rockfishes in the northeast Pacific Ocean reported by species.

	Major Features of Occurrences				
Species	Size (mmSL)	Area	Distance from shore (km)	Season	References*
S. aurora		San Francisco-central Baja CA	110-170	Apr-June	18
S. cortezi		Gulf of CA		Mar	15
S. crameri	9-10	Newport, OR	83-93	Apr-May	19
S. entomelas	10-15	off Oregon	9-306	Apr-May	9
S. flavidus	10-20	off Oregon	24-266	Apr-May	8
S. helvomaculatus	8-20	Newport, OR	83-120	July-Aug	19
S. jordani		San Francisco-San Diego	inshore	Jan-Feb	15
S. levis		California Bight		Jan-June	15
S. macdonaldi		central Baja CA		Mar	15
S. melanops	10-20	off Oregon	5-266	Apr-May	8
S. melanostomus	large	Los Angeles to Baja CA	5-220	Apr-Aug	14
S. paucispinis		CA to Baja CA	nearshore	Jan-Feb	15
S. pinniger	9-20	Newport, OR	83-120	Mar-June	19
S. zacentrus	7-10	off Oregon	46-148	Aug	9

* Numbers key to references in Literature Cited.

Collections of larvae identified as Sebastes spp. (rockfish) from the eastern Bering Sea, the northern Gulf of Alaska, and from off the Washington, Oregon, and California coast have been documented (Table 6). The following summarizes what we know about the distribution of rockfish larvae in these areas. Information based on the occurrences of larvae identified as rockfishes is of limited value, because several species are likely to be included in the collections, and each presumably has a specific pattern of distribution that overlaps those of other species.

Rockfish larvae are vulnerable to collection in plankton nets over a relatively narrow length range. Moser and Butler (in press) found that among over 11,000 rockfish larvae from California Cooperative Oceanic Fisheries Investigations (CalCOFI) plankton collections nearly 50% were less than 5 mm SL, and more than 90% were less than 7 mm SL. In plankton samples taken off Washington, Oregon, and northern California from March through November, little difference in mean size of the larvae was found; they ranged from 4.29 mm in November to 5.61 mm in March-June, and 5.22 mm in August (Northwest and Alaska Fisheries Center (NWAFC) files). Apparently, there is a severe mortality of larvae less than 7 mm, or their avoidance ability increases dramatically at that size. Notochord flexion and the concomitant development of the caudal fin occurs at about 7-8 mm in most species, so increased escapement of larger larvae is probable. Lengths of rockfish larvae have not been reported from other studies, but based on the above nearly all are probably less than 10 mm. Larger larvae and pelagic juveniles of at least some species are collected in neuston nets, where in eight surveys off Washington, Oregon, and northern California the mean length of the 1,112 rockfishes caught was 19.25 mm (NWAFC files).

One consequence of the small size of rockfish larvae in plankton collections is that the larvae are close in time and position to where they were released from the females. Thus, distribution of larvae can probably be used to give a fairly accurate idea of where and when release occurs. Off southern California most rockfish larvae are found in winter; off Washington, Oregon, and northern California most are in spring and summer; and in the Gulf of Alaska and in the Bering Sea most are in summer. Thus, it seems that release of larvae occurs progressively later in the year proceeding from south to north. This agrees with information already cited on seasonality of reproduction based on studies of gonads. The shift in timing of larval release may reflect the seasonal development of oceanographic conditions conducive to producing food suitable for the larvae.

Juvenile Identification

The transition from larval to juvenile stage often is defined to occur when counts of fin rays, gill rakers, and lateral line pores reach adult levels. This stage occurs in many species of rockfish at about 20 mm. Some species do not become juveniles until about 30 mm. Using this definition, many specimens reported as juveniles in the literature and this paper are actually large larvae.

Until the last decade the majority of specimens of juvenile rockfish were identified as Sebastes spp. Several workers have advanced the

Table 6.--Summary of data on *Sebastes* spp. larval collections from major ichthyoplankton programs in the eastern Bering Sea and the northeast Pacific Ocean.

Area	Reference	Years sampled	Months sampled	No. of cruises	collecting stations	*Sebastes* spp. occurrences
Eastern Bering Sea	Waldron [1981]	1955-79	All, mostly Spring--Summer	43	2,435	At 89 stations on 10 cruises, in spring and summer mainly near shelf break, mostly south of 60° N.
	Walline 1981	1979	June-July	1	114	In over 50% of oblique bongo tows throughout sampling area-mainly near shelf break south of St. Matthew's Island.
	Haryu et al. 1985	1970-79	June-August	14	418	592 larvae caught, throughout the southeastern Bering Sea.
Gulf of Alaska	Kendall and Dunn 1985	1972, 1977-79	All except Dec and Jan	11	707	Found late spring through early fall, peak in summer, shift inshore as season progressed.
Washington-Oregon-N. California	NWAFC files*	1980-84	Mar-June, Aug, Oct-Dec	8	873	Nearly equally abundant spring and summer. less abundant in fall, mainly offshore beyond Continental Shelf.
Oregon	Richardson et al. 1980	1972-75	March-April	6	306	Mainly beyond Continental Shelf.
California-Baja California	Ahlstrom et al. 1978**	1950-75	All	157	26,619	Most in winter, decrease abundance in southern part of area, mostly nearshore.

* Kendall, A.W. Jr. pers. comm. Dec. 1986.

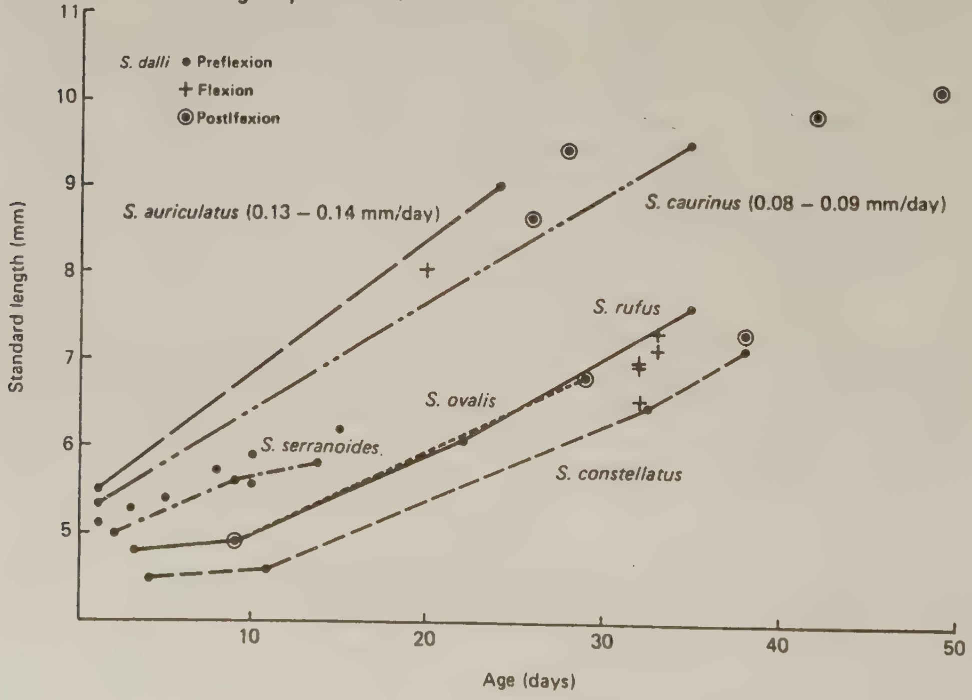
** Loeb et al. 1983 contains more detailed analysis of data from 1975. Other references cited therein contain additional analysis of CalCOFI data.

state of the art so now we can identify most juveniles captured off Washington, Oregon, and California. We were able to identify more than 99% of specimens of juvenile rockfish collected by midwater trawl off central California. Important papers on identification are Laroche and Richardson (1979 and 1980), Moser and Ahlstrom (1978), Moser et al. (1977), Moser and Butler (1981), Moser and Butler (in press), Moser et al. (1985), and Richardson and Laroche (1979). The preceding studies used material collected at sea or from rearing studies. Investigators employing scuba have conducted several nearshore studies of juvenile rockfish off California. Anderson (1983), who includes photographs of 17 species, is the most complete source on identification of juveniles in nearshore areas. The Tiburon Laboratory has developed a key that uses pigmentation patterns and meristics. Laroche is preparing a well-illustrated identification guide. Pelagic juveniles of 37 species will be illustrated in the laboratory guide being prepared by Matarese et al. (in press).

Larval and Juvenile Growth

Little is known about growth of rockfish larvae and juveniles. Under laboratory rearing conditions, change in length with time has been noted for larvae of seven northeast Pacific species. Only S. dalli lived beyond 40 days and a length of 10 mm. There is quite a wide variation shown in growth with some larvae reaching 9 mm in 24 days, while others were only a little over 7 mm after 38 days (Fig. 5). Since larval rearing has not been routinely successful in rockfishes, it is unknown how closely these growth rates reflect those found in the wild, or how much variation is due to different responses to rearing conditions.

Figure 5.--Growth of northeast Pacific rockfishes based on several rearing experiments.



Boehlert (1982) and Boehlert and Yoklavich (1983) held field-collected pelagic juvenile *S. diploproa* and benthic juvenile *S. melanops* under a variety of laboratory conditions of food, temperature, and photoperiod and noted effects on growth using stepwise multiple regression. Growth rate generally increased with increased ration; it was maximal at intermediate temperatures in *S. diploproa*, but continued to increase at higher temperatures in *S. melanops*. The temperature of maximal growth increased with fish size in *S. diploproa*. Growth rates observed in the laboratory under satiation rations were similar to those reported in the field (Boehlert and Yoklavich 1983).

Daily growth increments have been observed on the otoliths of a few juveniles of two species found in albacore stomach contents. The juveniles ranged in length from 15 to 31 mm and in age from 47 to 101 days. The growth rate, determined by otolith aging, of 21 field-collected juvenile (9.0-42.7 mm) *S. diploproa* (Boehlert 1982) was considerably less than that of the other two species so studied (Fig. 6). When these juvenile data are graphed along with data from reared *S. dalli*, a coherent picture emerges suggesting slow growth from 5 to 10 mm followed by more rapid growth through 30 mm, although *S. diploproa* growth seems to continue at a slower rate (Fig. 6). Median fin formation occurs in these species at about 10 mm and possibly the enhanced mobility this provides facilitates the observed increase in growth rate starting at this age.

Figure 6.--Growth or reared *Sebastes dalli* and size-at-age of field-collected juvenile *S. aurora*, *S. diploproa*, and *S. melanostomus*. Based on Boehlert (1982), Moser and Ahlstrom (1978), Moser and Butler (1981), and Moser et al. (1985).

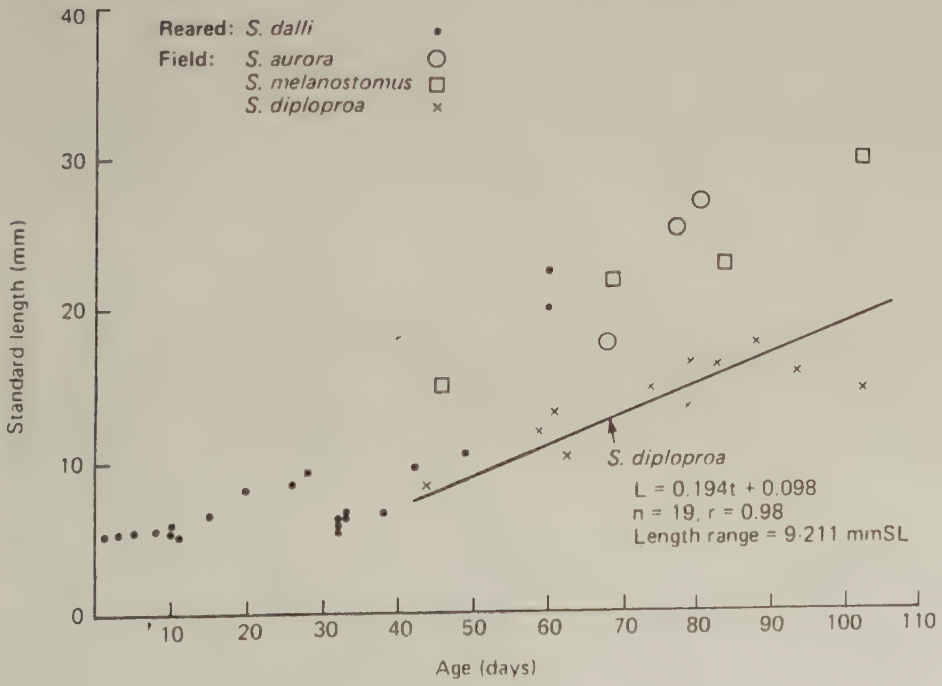


Table 8.--Catches of juvenile rockfishes by midwater trawls off of central California. A 25-m head rope length trawl with a 1.3-cm stretched mesh cod end was used. Towing depth varied from 10 to 100 m. April was sampled 1985 and 1986. Late May and June were sampled 1983-1986. (N = number of juveniles, 0 = number of occurrences, Y = number of years of occurrence). (Personal communication P. Adams, W. Lenarz, S. Moreland and T. Wyllie Echeverria, Southwest Fisheries Fisheries Center, Tiburon, California).

Month	April			Late May-June		
Number of Tows		48			357	
Species	N	0	Y	N	0	Y
S. auriculatus	205	12	1	532	83	2
S. caurinus 1/	0	0	0	9	6	1
S. crameri	0	0	0	15	10	2
S. diploproa	1	1	1	3	3	1
S. entomelas	0	0	0	15,335	99	4
S. flavidus	0	0	0	893	86	4
S. goodei	460	21	2	603	57	3
S. hopkinsi	1	1	1	1,374	41	3
S. jordani	134	17	2	84,828	180	4
S. levis	0	0	0	1	1	1
S. melanops	0	0	0	99	23	3
S. miniatus	1	1	1	0	0	0
S. mystinus	11	7	2	2,817	47	3
S. nigrocinctus	0	0	0	3	2	1
S. paucispinis	7	6	2	1,029	81	3
S. pinniger	16	8	2	242	65	3
S. rastrelliger	0	0	0	1	1	1
S. saxicola	16	10	2	65	22	3
S. semicinctus	0	0	0	10	7	2
S. serranoides	0	0	0	12	5	2
S. serriceps	0	0	0	3	3	1
S. wilsoni	4	3	1	20	8	3

1/ Specimens classified as *S. caurinus* could also be *S. carnatus*, *S. chrysomelas*, or *S. maliger*.

hopkinsi, *S. jordani*, *S. mystinus*, *S. paucispinis*, and *S. pinniger*. Peak catches of most species occurred in late May-June, but *S. auriculatus*, *S. goodei*, and *S. saxicola* are more abundant in April. They did not capture *S. rufus*, which is abundant in their area. In addition to the list of species collected as juveniles in Tables 7 and 8, *S. helvomaculatus* is reported by Richardson and Laroche (1979), *S. macdonaldi* by Moser (1972), *S. melanostomus* by Moser and Ahlstrom (1978), and *S. zacentrus* by Laroche and Richardson (1980).

Studies have found newly transformed benthic juveniles of many species both in nearshore and offshore waters. Anderson (1983) provides data on the timing of settlement in the nearshore habitat off central California for 15 species (Table 9). His data indicate that *S. entomelas*, *S. goodei*, *S. jordani*, and *S. paucispinis* only occasionally used this study area. The remaining 11 species regularly used the area. He also obtained a few specimens of *S. semicinctus* and *S. rosaceus*. Feder et al. (1974) report juvenile *S. atrovirens*, *S. miniatus*, *S. mystinus*, *S. paucispinis*, and *S. rastrelliger* in kelp beds off southern California. Hobson (pers. commun. Sept. 1986, Southwest Fisheries Center, Tiburon, California) has found significant numbers of *S. caurinus*, *S. flavidus*, *S. melanops*, and *S. mystinus* in kelp beds of northern California. Turner et al. (1969) found juvenile *S. auriculatus*, *S. caurinus*, *S. dalli*, and *S. serranoides* associated with man-made reefs in nearshore waters off southern California.

Sherwood and Mearns (1981) captured large numbers of juvenile *S. saxicola*, *S. diploproa*, and *S. jordani* using a bottom trawl off southern California. Moser and Ahlstrom (1978) captured benthic juvenile *S. melanostomus* off southern California. Chen (1971) captured juvenile *S. rosenblatti* and *S. umbrosus* on the bottom off southern California.

Table 9.--Number of juvenile rockfish in nearshore waters (<25 m) off central California (Anderson 1983).

	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
S. atrovirens	0	0	0	0	0	56	50	88	47	90	35
S. carnatus - *S. chrysomelas*	0	0	0	2	82	312	91	43	20	7	0
S. caurinus	0	0	46	95	207	115	7	67	27	4	0
S. entomelas	0	0	0	0	11	17	5	0	0	0	0
S. flavidus	0	0	9	14	141	119	76	32	22	51	1
S. goodei	0	0	0	0	6	0	1	1	0	0	0
S. jordani	0	0	0	0	5	6	2	0	0	0	0
S. melanops	0	0	3	6	113	68	44	20	9	20	0
S. miniatus	18	6	4	5	7	6	28	19	16	3	0
S. mystinus	0	0	13	101	326	129	77	40	36	9	0
S. paucispinis	2	2	6	18	59	14	10	8	8	4	0
S. pinniger	0	0	15	154	130	111	17	35	38	22	0
S. saxicola	0	0	14	3	59	117	214	100	109	0	0
S. serranoides	0	0	4	19	144	82	42	49	11	10	7

Love and Lee (1974) report on *S. rubrivinctus* caught by bottom trawl off Santa Barbara. Lenarz et al. (pers. commun. Sept. 1986, Southwest Fisheries Center, Tiburon, California) captured juveniles of 11 species with a bottom trawl off central California (Table 10). *S. saxicola* was particularly abundant. Apparently, midwater trawl gear does not adequately sample *S. crameri*, *S. saxicola*, and *S. semicinctus* in April-June off central California (Tables 8 and 10). Benthic juveniles of *S. flavidus* and *S. melanops* were collected off Oregon by Laroche and Richardson (1979); *S. entomelas* and *S. zacentrus* by Laroche and Richardson (1980); and *S. crameri*, *S. helvomaculatus*, and *S. pinniger* by Richardson and Laroche (1979). Carlson and Haight (1976) report that juvenile *S. alutus* begin settling in Alaskan fiords when they reach around 40-55 mm in length. *S. alutus* do not appear to settle until their second year of life.

May, June, and July are important months for juvenile rockfishes off Washington, Oregon, and California, when the young fish are important forage items for other fish (Merkel 1957) and for birds (Wiens and Scott 1975) and are at peak abundance in midwater catches (Table 7 and 8). Also, most major species transform to benthic juveniles during this time. Anderson (1983) reports peak catches of small benthic juvenile *S. flavidus*, *S. melanops*, *S. mystinus*, *S. paucispinis*, and *S. serranoides* during June (Table 9). These catches suggest that June is the peak month of transfer from the pelagic to nearshore stage for these species. Hobson (pers. commun. Sept. 1986, Southwest Fisheries Center, Tiburon, California) has found during the past 10 years that *S.*

Table 10.--Catches of juvenile rockfishes by 30 bottom trawls off of central California during June 1984. A 12-m head rope length trawl with a 1.3-cm stretched mesh cod end was used. Bottom depths were less than 200 m. (N = number of juveniles, O = number of occurrences) (Personal communication W. Lenarz, S. Moreland and T. Wyllie Echeverria, Southwest Fisheries Center, Tiburon, California).

Species	N	O
S. auriculatus	1	1
S. constellatus	1	1
S. crameri	17	4
S. flavidus	5	3
S. hopkinsi	12	2
S. jordani	3	2
S. paucispinis	1	1
S. pinniger	10	3
S. saxicola	201	12
S. semicinctus	7	3
S. wilsoni	2	2

flavidus, S. melanops, and S. mystinus first begin recruiting to nearshore habitats of northern California between late May and late June. Hobson's observations also provide some insight into other aspects of the juvenile stage. He has observed that the size of newly recruited juveniles is noticeably larger in some years than others. This suggests that size is not the only factor that triggers transition from one juvenile stage to another. He also has observed that during some years recruitment of these species to the nearshore habitat is concentrated into a period of less than a month, whereas during other years it is spread over several months.

Juvenile Field Studies

A study of rockfish recruitment was initiated in 1983 by the Tiburon Laboratory. Reports are available on progress through 1985 (Lenarz and Moreland 1985, Hobson et al. 1986). This section reviews these reports and adds some information obtained in 1986.

The study has three major objectives. The first is to develop methods for predicting year-class strength for economically important species of rockfish. Most species of rockfish are not recruited to fisheries until the age of 4-10 years. The study attempts to estimate year-class strength in the first year of life, and thus give fishermen and managers a basis for planning. The goal is to detect severalfold changes in year-class strength. Such precision has been shown to be appropriate for management purposes (e.g. Lenarz 1971). The study area originally included the coastal and offshore waters between Point Sur and Cape Mendocino, California. Beginning in 1986, the offshore work was limited to the area between Monterey and Bodega Bay. The study emphasizes seven species of rockfish that are important in the area: S. entomelas, S. flavidus, S. goodei, S. jordani, S. melanops, S. mystinus, and S. paucispinis.

The second objective is to gain a better understanding of factors that affect strength of recruitment, the most important factor underlying the success of fisheries. Although there must be a relationship between recruitment strength and the quantity and quality of eggs or larvae produced by adults, that relationship is obscured by poorly understood environmental factors. The Tiburon Laboratory is studying annual changes in reproductive physiology of adults, the relationship between oceanic conditions and recruitment success, and the fine-scale timing of reproductive success (daily ages of juveniles).

The third objective is to develop a better understanding of the ecological niches of juveniles of important species. About 60 species of rockfish occur in California and about 20 species are fairly abundant in the study area. These closely related species are similar in appearance in the juvenile stage. The ecology of some juvenile rockfishes is fairly well known during the nearshore stage, but little is known about the ecology of any species during the pelagic juvenile stage. We are studying feeding habits and environmental factors that affect distribution of pelagic juveniles, as well as adding to the existing knowledge of the nearshore stage.

Samples in the offshore area are collected with a midwater trawl that is slightly modified from the gear used by Mais (1974). The net has a 25-m headrope and 1.3-cm mesh liner in the codend. Tows 15 minutes in duration are made during darkness. Daylight tows were tried and discontinued because of low catches. Standard warp is 30 m for tows in depths less than 92 m and 90 m in deeper waters. Replicate tows are made at some stations for comparative purposes. Most of the work is conducted from late May through the end of June, but some work is done in April.

Analysis of replicate midwater tows made at some stations indicated that only one tow per station was necessary. The 90-m warp catches were larger than the 30-m warp catches, but the differences were not statistically significant. The power of the test was low because of small sample sizes. However, catches at these two depths were significantly correlated. We are collecting more data on depth distribution.

Midwater catches were lowest in 1983 and highest in 1985. Catches were similar in 1984 and 1986. An analysis of variance produced significant differences between 1984 catches and 1985 catches of *S. flavidus*, *S. goodei*, *S. jordani*, and *S. paucispinis*, but not *S. entomelas*.

Previous to 1986 one set of midwater trawl stations was occupied between Point Sur and Cape Mendocino. The 1985 season demonstrated to us that settlement can occur in late May-early June. We thus narrowed the area to Point Sur to Bodega Bay and will attempt to sample all stations three times during the season. The highest replicate will be used for the index of abundance.

Results from *Oncorhynchus tshawytscha* and nearshore *Ophiodon elongatus* stomach content analyses are promising. We believe that we may be able to eventually replace midwater trawl surveys with stomach content analyses to produce routine indices of abundance for important species of juvenile rockfish.

Scuba surveys are made in shallow nearshore waters of northern California's Sonoma and Mendicino coasts. The laboratory conducts scuba surveys to about 35 m every 2 to 3 weeks as weather permits. Two or three divers equipped with marking slates note numbers of juveniles during timed segments along random courses in representative habitats.

The nearshore studies are providing data on two species that do not appear to be sampled well by the midwater trawl survey, *S. melanops* and *S. mystinus*. In addition, the nearshore results are similar to the offshore results for *S. flavidus*. Statistically significant differences were found in 1983, 1984, and 1985 for *S. flavidus*, *S. melanops*, and *S. mystinus*.

The Laboratory began work on adult reproductive physiology and daily age determinations during the past year. It is premature to present a progress report on these two studies.

The Tiburon Laboratory plans to follow the basic field plan for the next several years. We intend to make statistical comparisons of the midwater trawl and stomach content data in a few years. We will drop the midwater trawl work if the stomach data appear to be adequate. We are attempting to obtain another vessel during May-June to examine some questions we have on the relationship between oceanic conditions and the distribution of the juvenile rockfishes.

It will be a number of years before we know how well the indices of abundance perform as predictors of year-class strength. However, there is already some evidence that indices will produce satisfactory results for S. paucispinis.

Implications for Management

Adult biomass estimation

The lack of pelagic eggs in rockfishes has several consequences for fisheries scientists. The use of surveys of pelagic eggs to estimate spawning biomass of fish populations is becoming a standard practice in several fisheries. This technique has been considered for several decades, and now is reaching a level of sophistication that makes it the method of choice for population estimates in several cases. Since rockfishes do not have pelagic eggs, this method cannot be considered for these fish. The pelagic larvae of fish can be used to estimate spawning biomass, but as the time between spawning and collecting increases, the effects of mortality and dispersion make the estimates less and less reliable. This method could be considered for rockfishes known to have very distinctive early larvae (e.g. S. jordani and S. paucispinis); however, early larvae of most rockfishes all look quite similar and it may not be possible to identify them routinely in plankton samples. To use eggs or larvae for a population estimate, details of reproductive parameters such as fecundity and distribution of spawning must be known rather precisely. This information is being accumulated for rockfishes, but is not yet generally available for these applications.

Larval identification

Since there are so many rockfishes in the northeast Pacific, and since larvae of few of them appear to be readily identifiable, their use in recruitment studies seems doubtful in the near future. Larval series (illustrations of a yolk-sac and/or preflexion larva, a flexion larva, and a postflexion larva) are only known for 9 of the 71 species. Among these are four species with distinctive larvae (S. aurora, S. jordani, S. melanostomus, and S. paucispinis), but the others may be confused with species that have not yet been described. Descriptions of larvae of other species are accumulating slowly, and rearing of northeast Pacific rockfish larvae has proven difficult so far. A further complication to the larval identification problem is that most of the rockfish larvae collected in plankton surveys are too small (<8 mm) to have distinctive meristic characters. The critical stages for establishing series, those between flexion larvae and pelagic juveniles (which have distinctive pigment patterns and adult meristic characters), are very rare indeed in plankton collections. It should be noted in particular that development of S. alutus, the most common and heavily fished rockfish in the Gulf of Alaska and Bering Sea, remains undescribed between the yolk-sac larvae and pelagic juvenile stages. While the use of rockfish larvae in fisheries studies is not impossible, scientists and managers should realize their limitations and gear expectations accordingly.

Longevity

The adult life histories of rockfishes are as varied as the early life histories. In this section we will discuss longevity, its effect on management, and implications for using estimates of year-class strength made during the year of birth.

S. jordani is a very abundant unexploited species (Lenarz 1980). It is relatively short-lived (rarely older than 10 years). This species could probably sustain relatively high rates of exploitation. Consequently, a fishery would probably be supported by one to several year classes. Early estimation of year-class strength is important for such a fishery because a year class only produces significant contributions to landings for a few years at most.

S. entomelas is a moderately-lived species (fish older than 30 years uncommon). The species supports moderate levels of exploitation (Hightower and Lenarz 1986). Strong year classes occur every few years. Uncertainty in the strength of incoming year classes has resulted in errors of about 25% in estimation of acceptable biological catch for the Pacific Fisheries Management Council.

S. alutus is a very long-lived species (oldest specimens approach 100 years). This species can only support low rates of exploitation (Ito et al. 1986), and stocks are depleted in most if not all areas. Fish do not fully recruit to the fishery until age 10 or more, and strong year classes occur only about once per decade. The ability to detect such year classes at an early age would provide managers and industry with a valuable planning tool.

While there is a wide range of longevity in rockfish, it appears that in general, management and industry would benefit from estimates of year-class strength at an early age. We hope to make such estimates from pelagic and nearshore surveys of juvenile rockfish densities.

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This paper was published too late to be included in our review. It contains an analysis of occurrences of rockfish larvae collected in the CalCOFI program, and discusses distributions of S. jordani, S. paucispinis, S. macdonaldi, and S. levis specifically.

DISTRIBUTION, FEEDING, AND GROWTH OF LARVAL WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*, FROM SHELIKOF STRAIT, GULF OF ALASKA

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AND G. W. BOEHLERT[4]

ABSTRACT

Walleye pollock in the Gulf of Alaska have recently been found to form an intense spawning aggregation in late winter in Shelikof Strait. This produces a dense patch of planktonic eggs in early April, and later in spring a patch of larvae that can be followed as it drifts to the southwest. The density of larvae observed in 1981 indicated that density-dependent effects on feeding may be important for larval survival. In May 1983 we conducted a field study to investigate spatial and vertical distribution, feeding, and growth of larvae from this spawning. During this study we found, in an area of maximum concentration (~ 1 larva m^{-3}) located by an initial survey, larvae averaged 11.1 mm SL, and were similar in size to those found elsewhere. The larvae in 1983 were larger, and less abundant than at the same time in 1981. Larval growth was estimated from the number of otolith daily growth increments at size of larva and was similar in the area of maximum concentration and in other areas. Larvae were concentrated vertically between about 15 and 50 m and showed a crepuscular pattern of increased density at 14-28 m during twilight. Neither the vertical nor horizontal patterns of larval occurrences seemed closely associated with particular values of temperature or salinity. Most larvae were found in a temperature range of 7.0°-5.5°C and a salinity range of 31.5-32.2‰. Guts of larvae collected during darkness contained less food than those from daytime. Copepod nauplii were largely replaced by *Pseudocalanus* spp. copepodids in the diet of larvae larger than 14 mm. At the densities of walleye pollock larvae observed in this study, it appears that zooplankton production in the area did not impact larval growth, even in the area of maximum density.

A large spawning concentration of walleye pollock, *Theragra chalcogramma*, was discovered in 1980 in Shelikof Strait, and subsequently a 220,000 metric ton/year fishery developed. Shelikof Strait, a 50 by 200 km body of water in the northern Gulf of Alaska, between the Kodiak Archipelago and the Alaska Peninsula, is apparently the major spawning center for Gulf of Alaska walleye pollock. Ichthyoplankton surveys in 1981 and 1982 showed that spawning occurs primarily in a restricted area within Shelikof Strait and over a short period of time, producing a dense patch of eggs. Thereafter, larvae drift southwest with prevailing currents (Fig. 1). The densities of walleye pollock eggs and early larvae found in Shelikof Strait in 1981 exceeded 50 m^{-3} (Dunn et al. 1984[5]), far greater than their densities in the Bering Sea (Kim and Kendall 1983[6]) or Funka Bay, Japan (Hayashi et al. 1968); moreover, these densities significantly exceed those reported for larvae of any other fish (Hempel 1979).

Energetic requirements of larvae in high densities may exceed production of food and possibly lead to density-dependent effects on larval growth and survival (Jones 1973). At larval densities frequently found (ca. 1 m^{-3}), density-dependent effects are not considered important (McGowen and Miller 1980; Cushing 1983). Laboratory studies, however, have demonstrated effects of stocking

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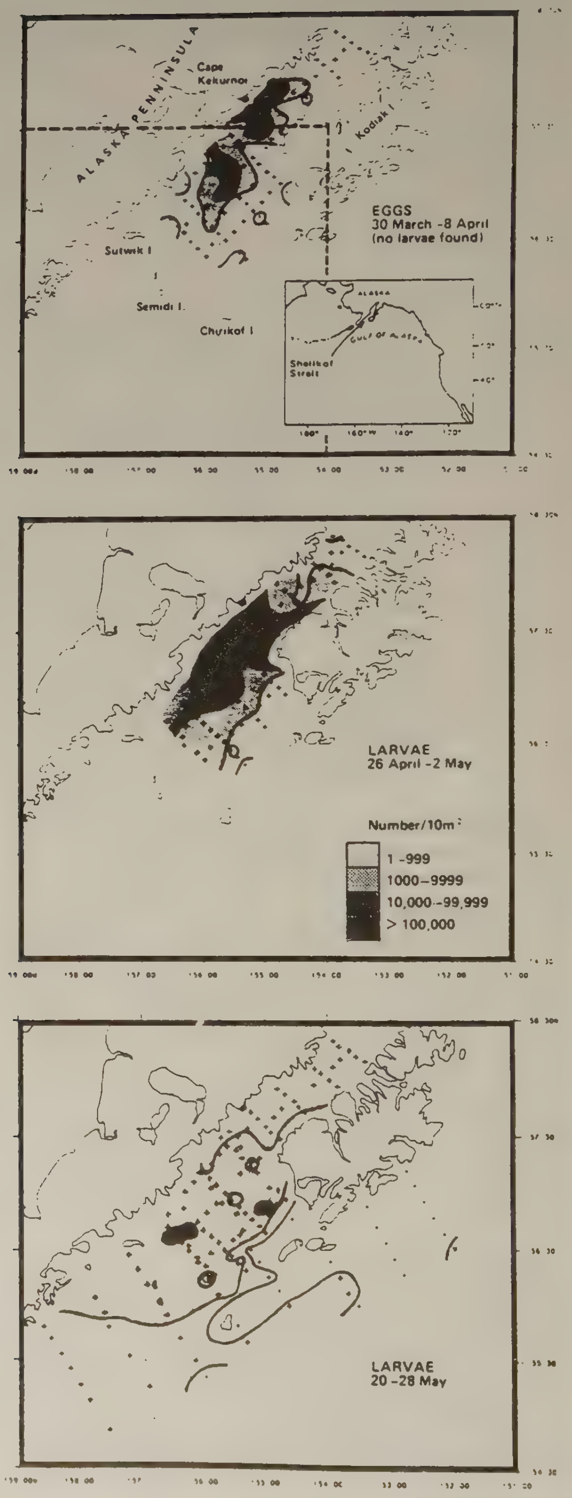
ALASKA PENINSULA
Cape Kekurnoi
Kodiak I
EGGS
30 March -8 April
(no larvae found)
Sutwik I
Semidi I.
Chirikof I
Shelikof Strait
GULF OF ALASKA
LARVAE
26 April -2 May
Number/10m²
1 -999
1000–9999
10,000–99,999
> 100,000
LARVAE
20 -28 May

FIGURE 1.—Distribution and abundance of walleye pollock eggs and larvae, spring 1981. Based on Bates and Clark (text fn. 9). Cape Kekurnoi is blackened as a point of reference. Area shown in Figures 2 and 6 is outlined is upper panel.

density upon growth (O'Connell and Raymond 1970; Houde 1975), and recent studies on patches of larvae co-occurring with prey suggest that enhanced growth may be observed at high prey concentrations in the field (Govoni et al. 1985). Search volumes of 5 mm larvae morphologically similar to walleye pollock are about 10 L per day (Laurence 1982); thus with densities of 1 larva in 25 L found in Shelikof Strait in 1981, it is possible that density-dependence is important in larval feeding rate and growth.

Walleye pollock is widely distributed in the subarctic North Pacific. Larval feeding habit studies have been conducted in Uchiura Bay, Hokkaido, Japan (Kamba 1977) and in the southeastern Bering Sea (Clarke 1978) where the principal prey has been found to be copepod nauplii with *Pseudocalanus* spp. becoming increasingly important as the larvae grow. Larval growth in the same areas has been studied by Hayashi et al. (1968) and Nishimura and Yamada (1984) for Hokkaido and by Walline (1985) and Clarke (1984) for the Bering Sea. Growth rates in field collections and laboratory rearing studies have been shown to be quite variable, from about 0.16 to 0.37 mm d^{-1} (Bailey and Stehr 1986).

We conducted a field study to investigate the ecology of larval walleye pollock in Shelikof Strait in May 1983 by locating and sampling the densest patch of larvae. Here we report on growth, feeding habits, and depth distribution of larval walleye pollock we collected.

METHODS AND MATERIALS

Field Collections

An ichthyoplankton survey of 63 stations on a 15 nmi (27.8 km) grid southwest of Kodiak Island, AK, was conducted aboard the NOAA ship *Chapman* from 21 to 28 May 1983 (Fig. 2). At each station a MARMAP double oblique bongo tow (Posgay and Marak 1980) was made from the surface to 200 m (as water depths permitted) with a 60 cm bongo net equipped with 505 μm mesh nets. Flowmeters were mounted in the net mouths and a bathykymograph was used to determine the maximum tow depth and to evaluate the tow profile. A neuston net (Sameoto and Jaroszynski 1969) with 505 μm mesh was also towed for 10 minutes at each station. The neuston net sample and one of the bongo net samples at each station were preserved in 5% sodium borate buffered formalin in seawater. Most walleye pollock larvae from the other bongo net were rough sorted at sea and were immediately preserved in buffered 90% ethanol for otolith examination.

The results of the sorting of larvae at sea were used to choose a location of high larval density for the diel feeding/distribution study (Fig. 2). Another oblique tow, after this survey, confirmed the presence of high concentrations of larvae. Several preliminary tows with four 20 cm bongo nets on the towing wire fixed at 10 m depth intervals (between 5 and 91 m) were made to find depths of maximum larval concentrations. A tow was then taken every 4 hours for 48 hours during 28-30 May 1983 with 20 cm bongo nets equipped with 253 μm mesh nets on one side and 333 μm mesh nets on the other. Four nets were fished simultaneously for 10 minutes at a ship speed of approximately 100 cm/second. The nets were placed on the wire to fish at four depths within the region of larval abundance (nominally 20, 30, 40, and 50 m). Flowmeters were mounted in the mouths of the nets, and a bathykymograph was deployed with the deepest net to record actual tow depths. During setting and retrieving, the ship maintained reduced speed to minimize fishing outside the chosen depth strata. Thus, although no closing devices were used, nearly all of the water passing into the nets was at the chosen depth (Kendall and Naplin 1981). Tows were made at 1030, 1430, 1830, 2330, 0230, and 0630 local time (sunrise was at 0455 and sunset 2138 h). During the sampling of the stations at 1430 and 0230 on both days, a 1 m^2 mechanical Tucker trawl with 505 μm mesh was fished for 10 minutes at 35 m to investigate escapement from the 20 cm bongo nets. Also during the second 24-h period a 60 cm bongo net with 505 μm mesh was fished about 2 m below the deepest 20 cm bongo net to stabilize the wire and allow further catch comparisons.

Expendable bathythermograph (XBT) casts were done at each survey grid station and at the 1430 and 0230 vertical distribution study stations. Conductivity-temperature-depth (CTD) casts (Ocean Data Equipment Corporation[7] Model 302) were made at 15 of the survey grid stations selected to provide three sections across the major southwesterly setting flow field in the area (Fig. 2).

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[7] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

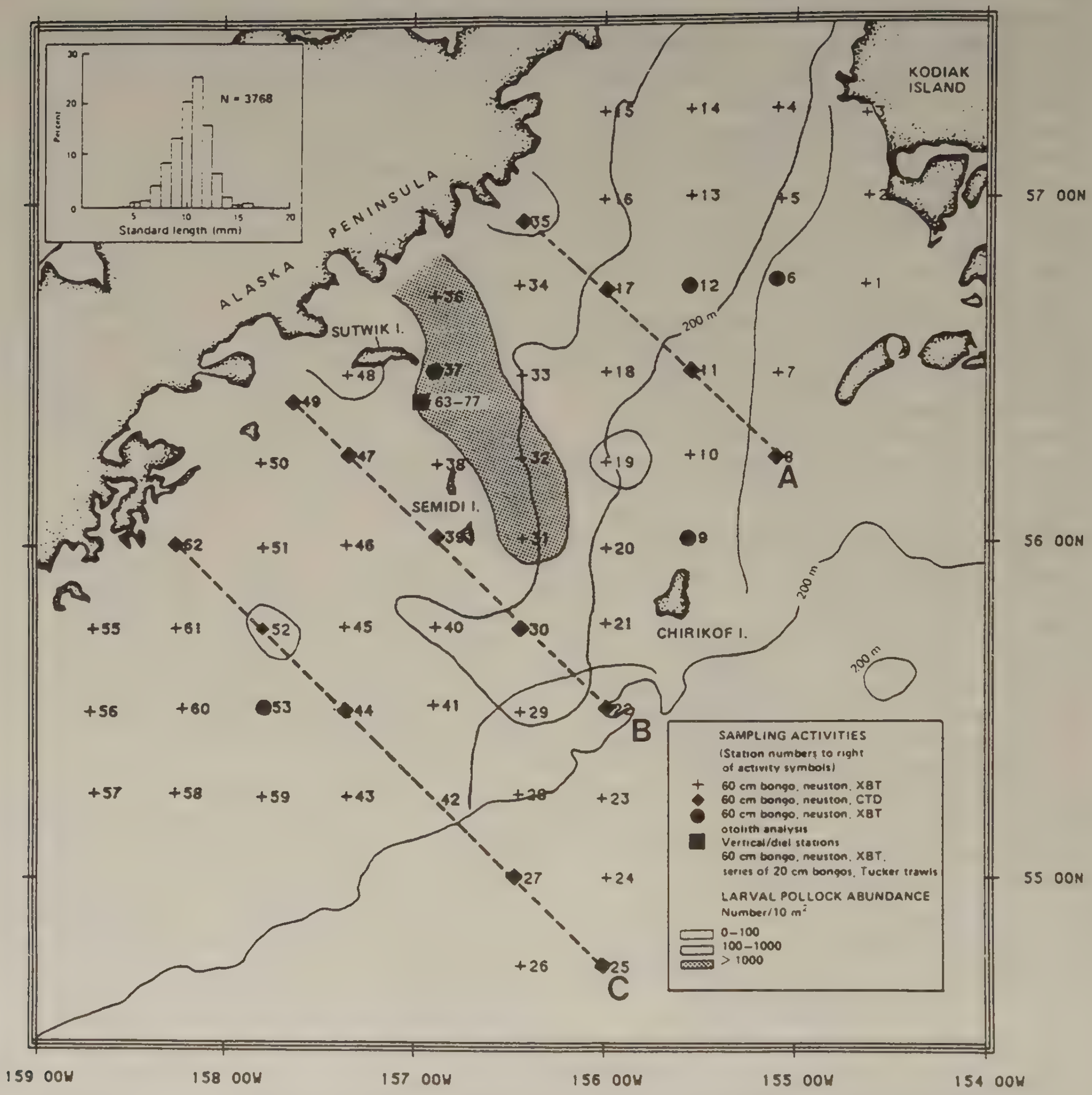
Percent
30
20
10
0
5
10
15
20
N = 3768
Standard length (mm)
ALASKA PENINSULA
KODIAK ISLAND
SUTWIK I.
SEMIDI I.
CHIRIKOF I.
200 m
+15
+14
+4
+3
+16
+13
+5
+2
35
+34
17
12
6
+1
+36
+48
37
+33
+18
11
+7
49
63–77
+50
47
+38
+32
+19
+10
8
A
62
+51
+46
39
+31
+20
9
+55
+61
52
+45
+40
30
+21
+56
+60
53
44
+41
+29
22
B
+57
+58
+59
+43
42
+28
+23
27
+24
+26
25
C
SAMPLING ACTIVITIES
(Station numbers to right of activity symbols)
60 cm bongo, neuston, XBT
60 cm bongo, neuston, CTD
60 cm bongo, neuston, XBT otolith analysis
Vertical/diel stations 60 cm bongo, neuston, XBT, series of 20 cm bongos, Tucker trawls
LARVAL POLLOCK ABUNDANCE
Number/10 m²
0–100
100–1000
> 1000
57 00N
56 00N
55 00N
159 00W
158 00W
157 00W
156 00W
155 00W
154 00W

FIGURE 2.—Distribution, abundance (numbers per 10 m^2) and lengths of walleye pollock larvae from 60 cm MARMAP bongo tows superimposed on sampling pattern used in the northern Gulf of Alaska, May 1983. Hydrographic sections are labelled A, B, C (see Figure 4).

Laboratory Procedures

Fish eggs and larvae were identified to the lowest taxon possible at the Polish Plankton Sorting Center in Szczecin, Poland. Fish larvae were measured to the nearst 0.1 mm standard length (SL); when more than 50 larvae of a taxon occurred in a sample, a random subsample of 50 was selected for measurement. Identifications were verified at the Northwest and Alaska Fisheries Center. For distributional analysis of fish eggs and larvae from the survey, numbers per tow for each taxon were converted to numbers under 10 m^2 of water surface using volumes of water filtered and maximum tow depth (see Smith and Richardson 1977). To compare relative abundances of various taxa, an estimate of the total number of eggs or larvae of each taxon present in the entire survey area was derived by summing the catches at each station and multiplying by the area of sea surface represented by that station (the Sette-Ahlstrom method, see Smith and Richardson 1977). This estimate was thought to make best use of all the available data.

A chi-square test analyzed differences in the numbers of walleye pollock larvae caught as a function of time of day and depth at the diel station. For this test, numbers of larvae in the two sides of the 20 cm bongo nets were combined. Also, catches at the same time and depth but on different days were combined when complete depth series were collected. Four out of six times two complete depth series were collected; at two times only one complete depth series was collected.

Zooplankton were sorted, identified, and enumerated from subsamples of collections made with the 253 μm mesh net. The subsample was chosen such that at least 500 organisms were sorted from each sample.

For larval feeding analysis, 20 walleye pollock larvae (or the total sample when <20 were caught) were selected to represent the size range in the total sample from each of the 333 μm mesh, 20 cm bongo net samples. The guts were dissected from the larvae, and all food items in the foregut, midgut, and hindgut were teased out, identified, and counted.

Lengths and greatest widths were measured for all food items in the larvae collected at 0630, 29 May. Lengths used were carapace length for copepod nauplii, metasome length for copepodids, and total length for all other prey. These measurements were used to estimate volumes of prey organisms, which were applied to the rest of the samples. Mensuration formulae were used to calculate the volume of copepod eggs, copepod nauplii, copepodids of *Pseudocalanus* spp., *Acartia* spp., and *Oithona* spp. (Nishiyama and Hirano 1983; Table 1). *Pseudocalanus* spp. mensuration formulae were used to estimate the volumes of unidentified copepodids. The volumes of other food items were not estimated since their low abundance did not allow adequate measurement of body proportions.

Samples used for age and growth analysis were selected from one station within the area of highest larval density (Station 37, Fig. 2), and from four stations located outside of this dense patch. Standard lengths of larvae from as broad a size range as possible within each sample were measured to the nearest 0.1 mm using an ocular micrometer. Both sagittal otoliths were removed and cleaned using a pair of fine needles under a dissecting microscope fitted with polarizing filters. Whole otoliths were affixed to microscope slides with clear histological mounting medium and increments read in the sagittal plane under a compound microscope with transmitted light at 1000× magnification. Most of the otoliths had a distinct distal-proximal curvature and readability was enhanced when the otolith was mounted with the concave side up.

Increments were identified as a pair of adjacent light and dark bands, formed concentrically around the focus. A prominent dark band surrounding the focus was observed on each otolith (Fig. 3). Since mean otolith diameter at this band (16.0 ± 0.13 μm SE) was similar to the diameter of otoliths from 1-day-old, laboratory-reared larval pollock (18.97 ± 0.37 μm, Nishimura and Yamada 1984; 16-20 μm, Walline 1983; 15.3 ± 1.2

TABLE 1.—Mensuration formulae (Nishiyama and Hirano 1983),[1] length to width ratios, metasome to whole body ratios, metasomal lengths, mean lengths, and mean diameters used to calculate volumes of copepodids, copepod nauplii, and copepod eggs in guts of larval walleye pollock in Shelikof Strait.

Species	K Length:width (this study)	m Metasome:whole body (Nishiyama and Hirano 1983)	Lm Metasomal length (this study)
Pseudocalanus spp.	2.239	0.97	0.870
Oithona spp.	1.824	0.93	0.189
Acartia spp.	3.213	0.95	0.916
Unidentified copepodids	2.539	0.97	0.870

[1] Mensuration formulae (Nishiyama and Hirano 1983):

Volume of copepodids = $\{Lm/6 \cdot (Lm/K)^2 \pi\}/m$.

Volume of copepod nauplii = $\left(\frac{\pi}{24} \text{ carapace length}^3\right)$;

mean carapace length = 0.187.

Volume of copepod eggs = $\left(\frac{\pi}{6} \text{ egg diameter}^3\right)$;

mean egg diameter = 0.110.

μm, Bailey and Stehr[8]), this band was presumed to be the hatching check and was counted as the first increment. Nishimura and Yamada (1984) found that increments were formed daily, beginning with the day of hatching, on the otoliths of laboratory-reared larval pollock. Similar observations have been made on larval walleye pollock otoliths viewed with both light and scanning electron microscopy by Bailey and Stehr (fn. 8). Increments were, therefore, considered to be deposited daily and increment counts were equated with the age of the fish in days after hatching.

The mean of two independent increment counts was used in growth rate analysis. Age-at-length data from each station were fitted separately with simple linear regressions. Analysis of covariance was used to compare growth rates and Dunnett's test of multiple comparisons identified significantly different rates (Zar 1974).

RESULTS

Hydrographic Observations

Temperature in the survey area varied from just above 7°C at the surface at some stations to slightly $<5°C$ in deeper shelf water (Fig. 4). Temperature gradually decreased with depth, and temperatures in the upper 50 m (where most of the walleye pollock larvae were found) were generally between 7.0° and 5.5°C. At the diel-vertical distribution station, temperatures were similar to those found throughout the area, although the temperature gradient was more uniform than elsewhere. In the upper 60 m at this station, tem-

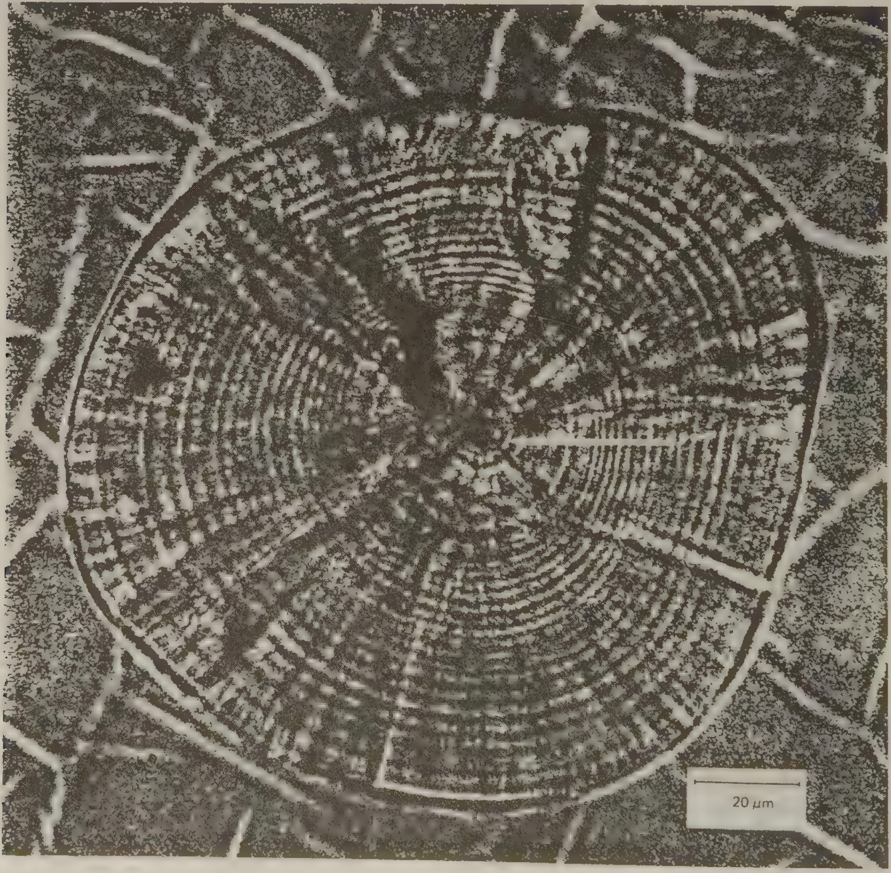

FIGURE 3.—Otolith from a 11.57 mm SL walleye pollock larva showing 27 daily growth increments. The arrow near the focus indicates the first increment. Scale bar indicates 20 μm.

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[8] K. Bailey and C. Stehr, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way, N.E., Seattle, WA 98115, pers. commun. 7 February 1985.

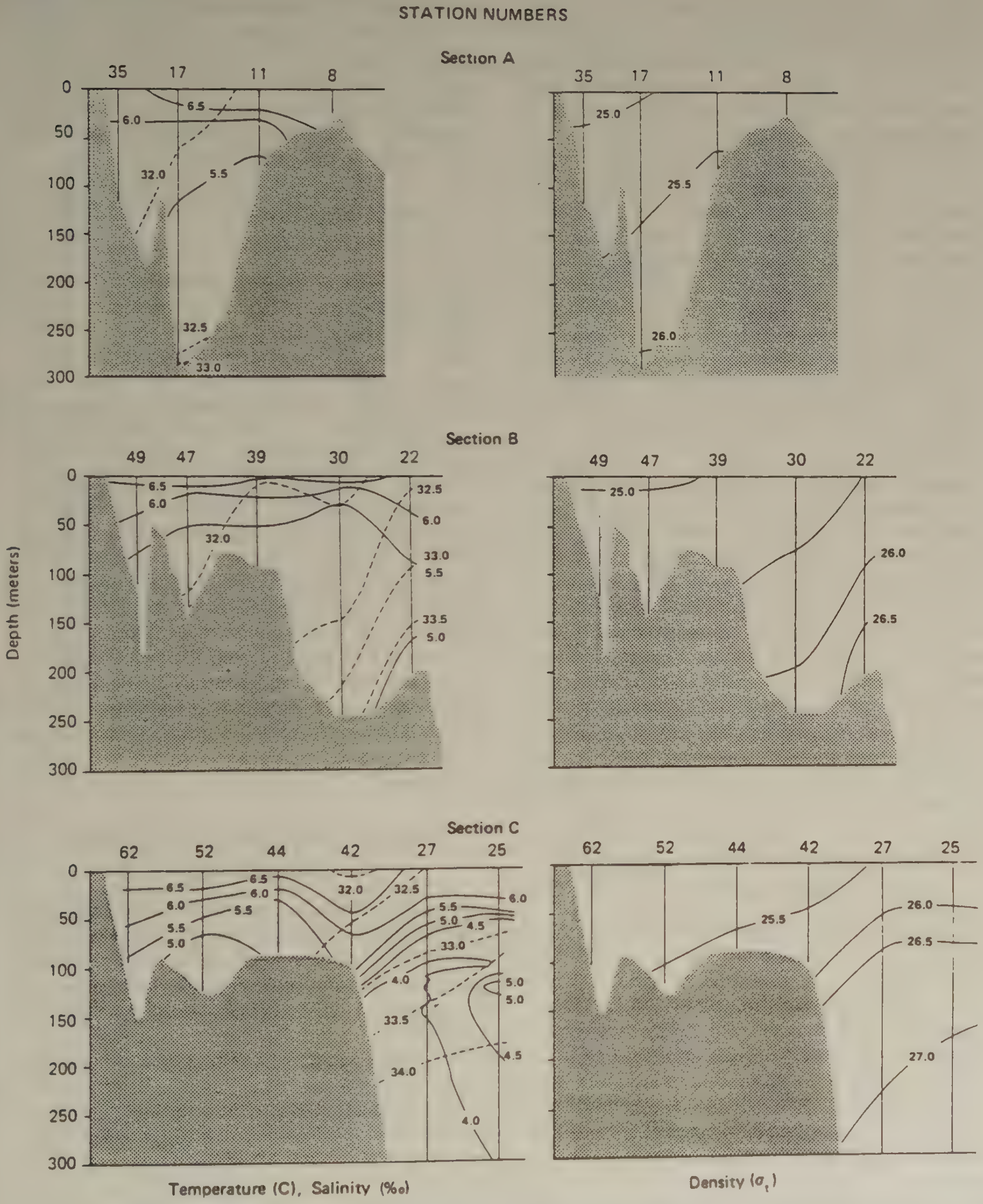

FIGURE 4.—Temperature (solid contours), salinity (broken contours), and density observed in three sections across the sampling area, May 1983. Station and section locations are shown in Figure 2.

perature steadily decreased from 6.9°C to 6.0°C, and at the bottom (120 m) the temperature dropped to 5.5°C. Among the four XBT casts (taken at 12-h intervals), the temperature at a given depth varied as much as 0.5°C: an isotherm depth varied vertically by as much as 50 m.

Salinity varied from 31.5 to >33.5‰ in the survey area. Lowest salinities were found at the surface toward the Alaska Peninsula, and high salinities were found offshore in deeper waters. Isohalines generally sloped from offshore to inshore. This slope was most pronounced at Section A, the one closest to Shelikof Strait. Most larvae were in water between 31.5 and 32.2‰. The salinity profile at the CTD station closest to the diel station showed a slight and steady increase in salinity with depth starting from a surface value of 31.8‰ and ending with a bottom (142 m) value of 32.1‰.

Density sections (σ_t) show the same sloping pattern as the salinity sections but are even more pronounced (Fig. 4). Values ranged from <25.0 at the surface near the Alaska Peninsula to >26.4 in deeper waters near the edge of the continental shelf. No sharp pycnocline was observed but rather a gradual increase in density with depth and distance from the Alaska Peninsula. Most walleye pollock larvae were in water with densities between 25.0 and 25.4 σ_t. The density profile observed near the diel station closely paralleled the salinity profile, with a gradual increase with depth from $\sigma_t = 24.9$ at the surface to $\sigma_t = 25.4$ at the bottom (142 m).

Relative Abundance of Eggs and Larvae

Neuston tows and bongo tows captured eggs of 13 and 14 taxa, respectively (Fig. 5). Rank orders of abundance, based on estimated total numbers of fish eggs in the neuston catches showed *Microstomus pacificus* (Dover sole) to be in greatest abundance, followed by *Glyptocephalus zachirus* (rex sole) and *Theragra chalcogramma*. In bongo catches, unidentified pleuronectid (righteye flounders) eggs were most abundant, followed by those of *M. pacificus*, *G. zachirus*, and *T. chalcogramma*.

Larvae of 29 and 42 taxa were identified in neuston and bongo catches. Rank order of abundance of fish larvae in neuston tows, based on estimated total numbers, showed *Ammodytes hexapterus* (Pacific sand lance) to be most abundant followed by *Hexagrammos decagrammus* (kelp greenling), *Lyconectes aleutensis* (dwarf wrymouth), *Bathymaster* spp. (ronquils), and *T. chalcogramma*. In bongo catches *T. chalcogramma* larvae were most abundant followed by those of *Bathymaster* spp., *A. hexapterus*, *Hippoglossoides elassodon* (flathead sole), and unidentified gadids (codfishes).

Distribution and Abundance of Walleye Pollock Eggs and Larvae

Eggs of walleye pollock were taken in 26% of the bongo tows and in 27% of the neuston tows but in low abundance. Only 262 eggs were collected. Some early stage eggs were collected, indicating recent spawning, but older eggs were also present. Eggs were found mainly in water over the deeper part of Shelikof Strait, with decreasing abundance to the southwest (Fig. 6).

Larvae of walleye pollock were found in 89% of the bongo catches and 24% of the neuston catches. The center of larval concentration was near the middle of the survey pattern (Fig. 2). Mean standard length of the larvae throughout the survey was 10.63 mm (range 3.8-21.3 mm, SD = 1.81 mm), with no differences in mean length by area. At each of five stations near Sutwik Island and the Semidi Islands, more than 1,000 larvae/10 m^2 were encountered. At 44 of the 64 stations, more than 100 larvae/10 m^2 were found. A total of over 10^{12} larvae was estimated to be present in the survey area.

Vertical Distribution of Walleye Pollock Larvae

In preliminary tows with the 20 cm bongo nets most larvae were caught above 60 m. During the vertical distribution study actual depths of sampling based on bathykymograph records covered the ranges of 14-20, 21-28, 28-38, and 39-47 m (Table 2).

The mean length of the larvae during our diel vertical distribution study was 11.1 mm SL. The range of mean lengths among the individual samples was 10.0-12.2 mm SL, and the range of standard deviations was 0.8-2.3 among hauls with more than 10 larvae. No patterns of size of larvae with depth or time of day were seen by visual inspection of the data, and since the range of mean lengths was so narrow, and the confidence intervals overlapped, no further analysis was performed.

There were no diel differences in catch rates

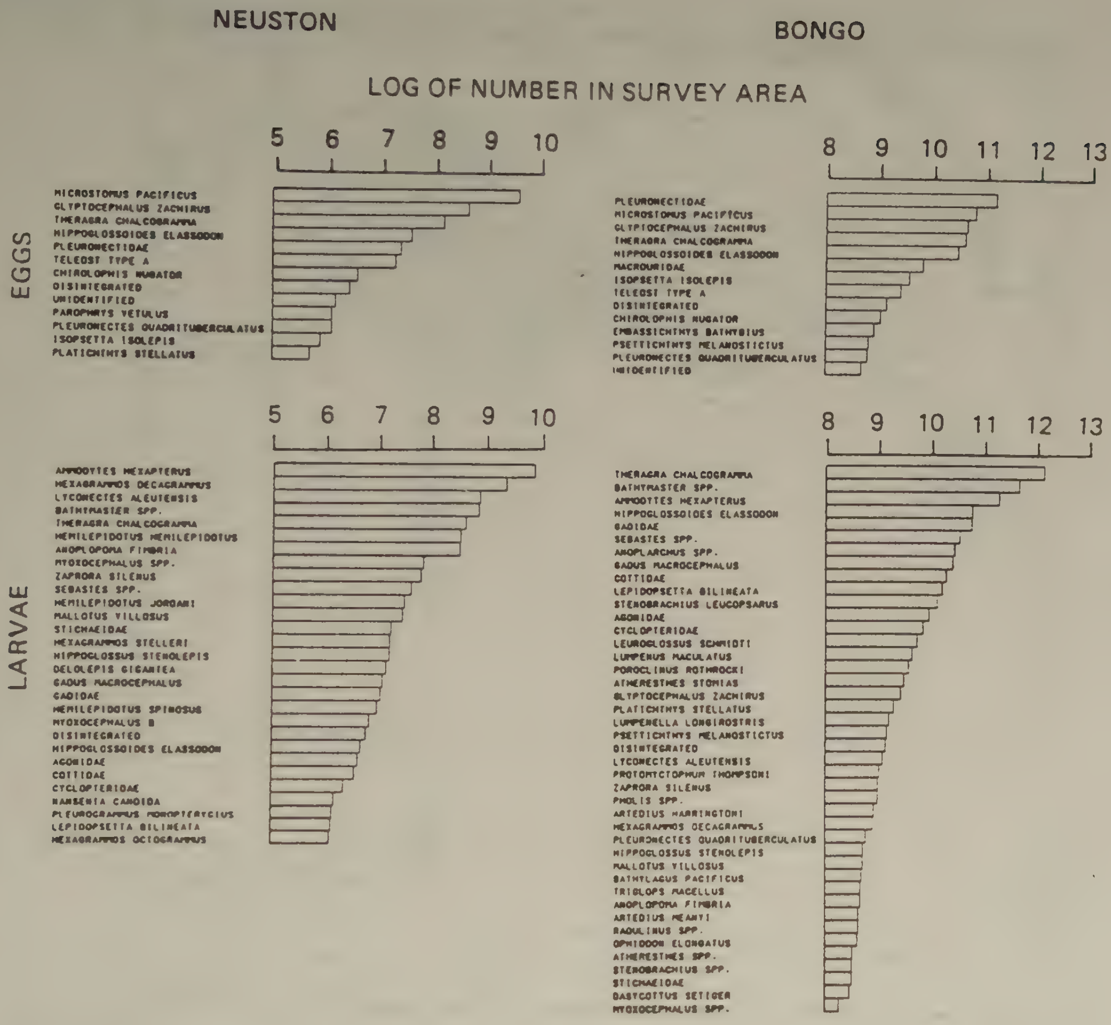

FIGURE 5.—Rank order abundance, as log of total numbers in the survey area, of fish eggs and larvae in neuston and bongo tows during the survey, May 1983.

TABLE 2.—Chi-square test of numbers of walleye pollock larvae with time and depth from the vertical distribution study, May 1983.

Depth (m)	Time 1840-1920		2235		0320-0238		0629-0635		1047		1432-1515	
	No. samples											
	16		8		16		16		8		16	
	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
14-19	76	(94)	98	(78)	133	(159)	100	(59)	61	(68)	37	(47)
21-28	76	(122)	138	(101)	202	(207)	68	(76)	108	(89)	65	(62)
28-38	110	(95)	11	(79)	201	(161)	46	(59)	87	(69)	56	(48)
39-47	136	(87)	83	(72)	140	(148)	35	(55)	33	(63)	43	(44)
Total	398		330		676		249		289		201	
χ^2	52.19		78.89		14.73		39.46		23.77		3.63	

Total χ^2 = 212.69 (15 df, $P < 0.005$)

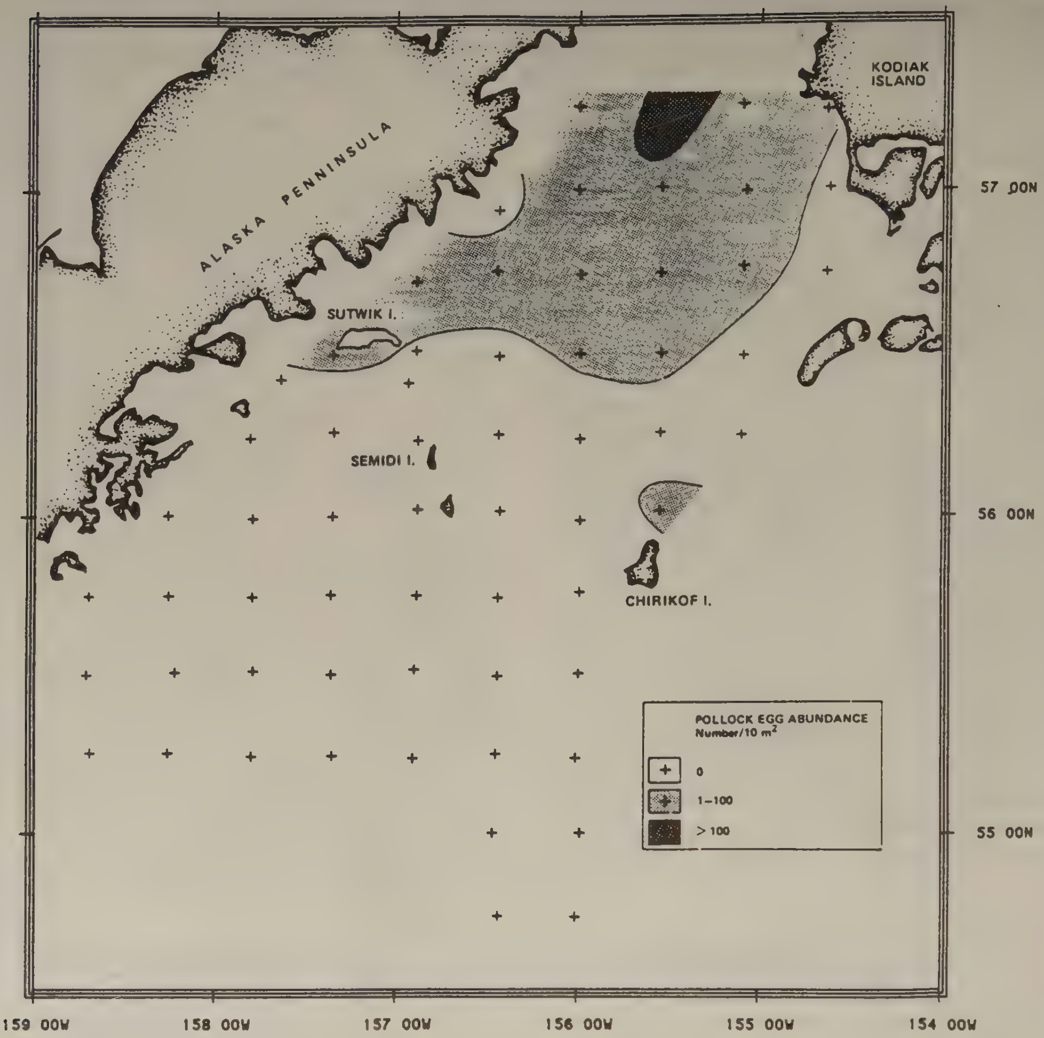
KODIAK ISLAND
ALASKA PENNINSULA
SUTWIK I.
SEMIDI I.
CHIRIKOF I.
57 00N
56 00N
55 00N
159 00W
158 00W
157 00W
156 00W
155 00W
154 00W
POLLOCK EGG ABUNDANCE
Number/10 m^2
0
1–100
> 100

FIGURE 6.—Distribution and abundance of walleye pollock eggs, May 1983.

(Table 2). The means of the catch per 10 m^3 at each time-depth combination expressed as a percentage of the total catch at that time of day suggests a pattern of limited diel vertical migration (Fig. 7). The chi-square test was highly significant ($P < 0.005$) indicating that the null hypothesis, that the larvae were distributed at each depth in the same proportions among the different times, should be rejected. Examining the relative abundances within each time period, the larvae appeared to be concentrated above 20 m at 0630 h, and at 28-47 m by 1830 h (Fig. 7). They were most evenly distributed in the early afternoon and most abundant in the 21-28 m stratum during darkness (2230 and 0230 h) and at 1030 h. The lowest percent abundance at each time period shows a complementary pattern, with relatively small catches at 39-47 m from 0230-1430 h. This pattern was observed on both days during the 48-h sampling.

In summary, it appears that some larvae gradually move up in the water column from a depth of 30-50 m in the evening to above 20 m in early morning. They gradually descend during daytime, and are most evenly distributed in the early afternoon.

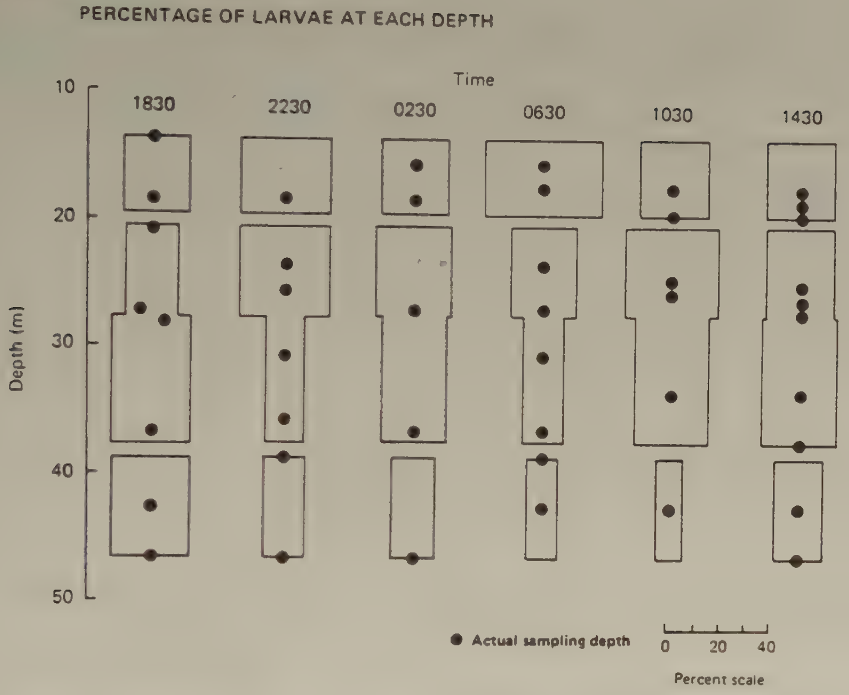

FIGURE 7.—Relative abundance as percent of larvae at each depth for each time interval, of walleye pollock larvae from the vertical distribution study, May 1983.

Comparison of Catches of Walleye Pollock Larvae by Different Gears

The sizes of larvae in the different bongo nets at the vertical distribution station were similar (Table 3). Mean lengths of larvae in the 20 cm bongo nets varied from 11.00 in the 333 μm mesh net to 11.10 mm in the 253 μm mesh net (SD = 1.76 and 1.69 mm respectively); mean length in the 60 cm bongo nets was 11.07 mm (SD = 1.77 mm). The Tucker trawl, however, caught larvae that had a mean length of 9.64 mm (SD = 1.67 mm). The overall mean abundance of larvae in the 20 cm bongo in the 28-38 m depth stratum nets (11.82 larvae/10 m^3) was similar to that in all the Tucker trawls (11.66 larvae/10 m^3) which were towed at 35 m. The mean of the catches in the 60 cm bongo nets, towed just below the deepest 20 cm bongo, was not notably different from the mean of those 20 cm bongo catches taken at the same times.

Variations in overall catches in the 20 cm bongo nets at the vertical distribution stations seemed to reflect the patchy nature of the concentration of larvae and not net avoidance related to time of day. The largest catches occurred during daylight, at 1030 h, while the smallest catches occurred during the time intervals immediately preceding (0630 h) and immediately following (1430 h) the largest catches. Since we sampled one geographic site rather than following a drogue, we probably sampled water with different concentrations of larvae as it drifted past us during the 48-h sampling. It appears that the larvae decreased from a concentration greater than 1 m^{-3} during the first 24 hours to <0.5 m^{-3} during the second 24 hours. The size of larvae did not change during the study again indicating that increased daytime net avoidance was not significant.

Hydrography in Relation to Distribution of Walleye Pollock Larvae

No obvious hydrographic features were associated with larval distributions. At the diel station, larvae were concentrated between 14 and 47 m where temperature within the upper 50 m was

TABLE 3.—Comparisons of catches and lengths (mm SL) of walleye pollock larvae with gear, time of day, and depth from the vertical distribution study, May 1983.

	mm SL (SD)	number	mm SL (SD)	number
	333 µm mesh		253 µm mesh	
Depth (m)				
14-19	11.13 (1.80)	333	10.86 (1.77)	333
21-28	11.07 (1.74)	405	11.07 (1.87)	427
28-38	11.24 (1.68)	232	11.04 (1.73)	290
39-47	11.19 (1.60)	249	11.17 (1.46)	229
Time (local)				
1830	11.03 (1.67)	210	10.86 (1.65)	118
2230	10.98 (1.58)	189	10.76 (1.56)	185
0230	11.50 (1.83)	315	11.39 (1.75)	361
0630	11.12 (1.42)	133	11.31 (1.82)	116
1030	11.01 (1.75)	331	10.61 (1.81)	301
1430	10.73 (1.57)	183	11.13 (1.72)	182
Gear				
20 cm bongos, 253 µm mesh	11.10 (1.69)	1,388		
20 cm bongos, 333 µm mesh	11.00 (1.76)	1,381		
All 60 cm bongos	11.07 (1.77)	578		
All Tucker trawls	9.64 (1.67)	2,180		

stable at 6.90°-6.15°C (Fig. 8). Nearby, salinity and density showed a very gradual increase with depth.

The pattern of water movement in the survey area, derived from the temperature and salinity observations, indicated a general southwest flow of water at all depths. In the area of larval concentration, most of the flow tended southward, following the deep trough from Shelikof Strait across the continental shelf between the Semidi Islands and Cherikof Islands (S. Kim[9]).

Diet and Feeding of Walleye Pollock Larvae

Eighteen different food items were identified in walleye pollock larvae sampled at the diel sta-

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[9] S. Kim, School of Fisheries, University of Washington, Seattle, WA 98195, pers. commun. September 1985.

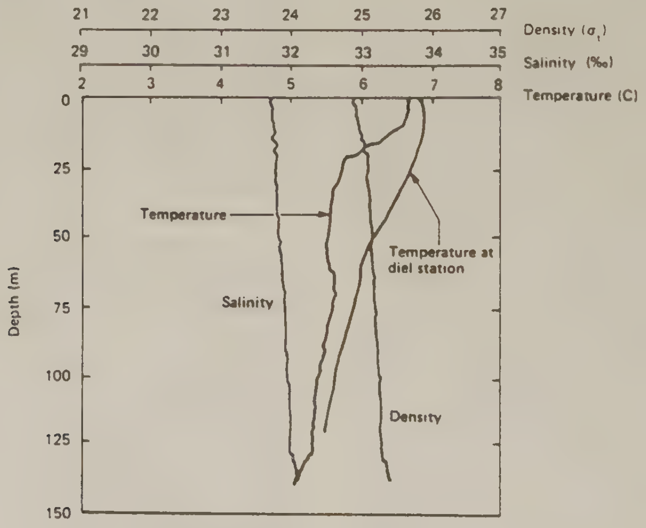

FIGURE 8.—Temperature, salinity, and sigma-t profiles at Station 47 with temperature profile from the diel station (Stations 63-77) shown for comparison. See Figure 2 for station locations.

tions. Copepod nauplii 90-600 μm in length and between 40 and 250 μm in width were the most abundant food item for larvae <14.0 mm (Fig. 9). The length- and width-frequency distributions of nauplii indicate that *Pseudocalanus* spp. and *Oithona* spp. are the likely prey taxa. Nauplii became numerically less important in diets of larger larvae. *Pseudocalanus* spp. copepodids, copepod eggs, and *Oithona* spp. copepodids made up a larger numerical portion of the food of these larger larvae (Fig. 10). The increased importance of *Pseudocalanus* spp. copepodids in the diet of larger larvae is evident in terms of gut volume (Fig. 10). Examination of the contribution of the copepod eggs to the diet indicates that while eggs increase numerically from 1.5% in the 8.0-8.9 mm size group to 55% in the 14.0-14.9 mm size group, their volume increases only from 0.5 to 3.6%.

The number of food organisms and mean prey volume per larva show a diel feeding pattern (Fig. 11). The maximum gut contents were observed during the afternoon. Collections at 2235, 0230, 0238, and 0629 have the lowest mean number of food items per larva, which suggests that feeding during darkness is reduced. The mean gut volumes show a similar pattern (Fig. 11). Although gut volume at 1047 h on 29 May was unusually low, it was not an indication of reduced feeding. Here the gut contents consisted of numerous copepod nauplii and few adult copepods. Thus the calculated prey volume is quite low, while the number of food items per gut is high.

Zooplankton Composition

Thirty-nine groups of zooplankters were identi-

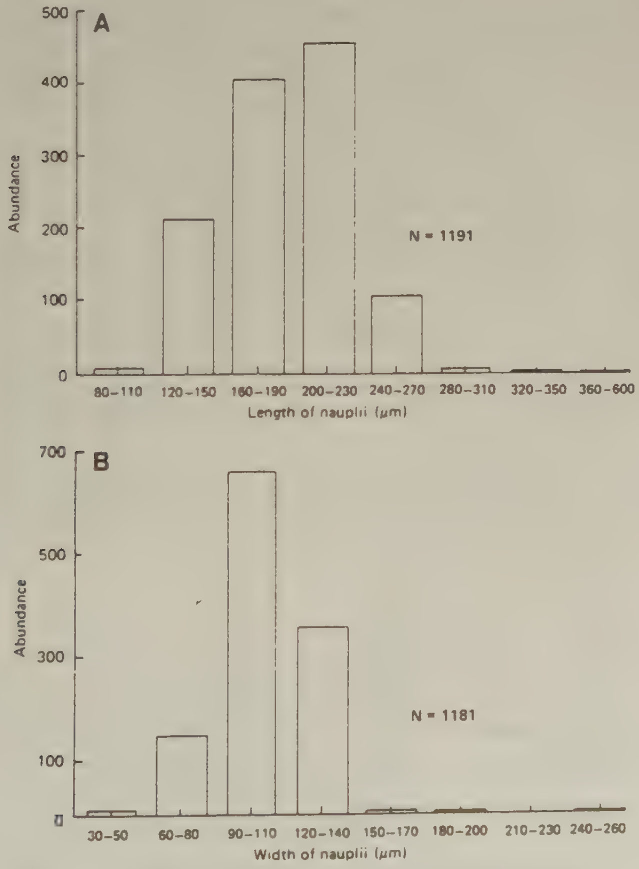

FIGURE 9.—Length (A) and width (B) size-frequency distribution of copepod nauplii from guts of walleye pollock larvae.

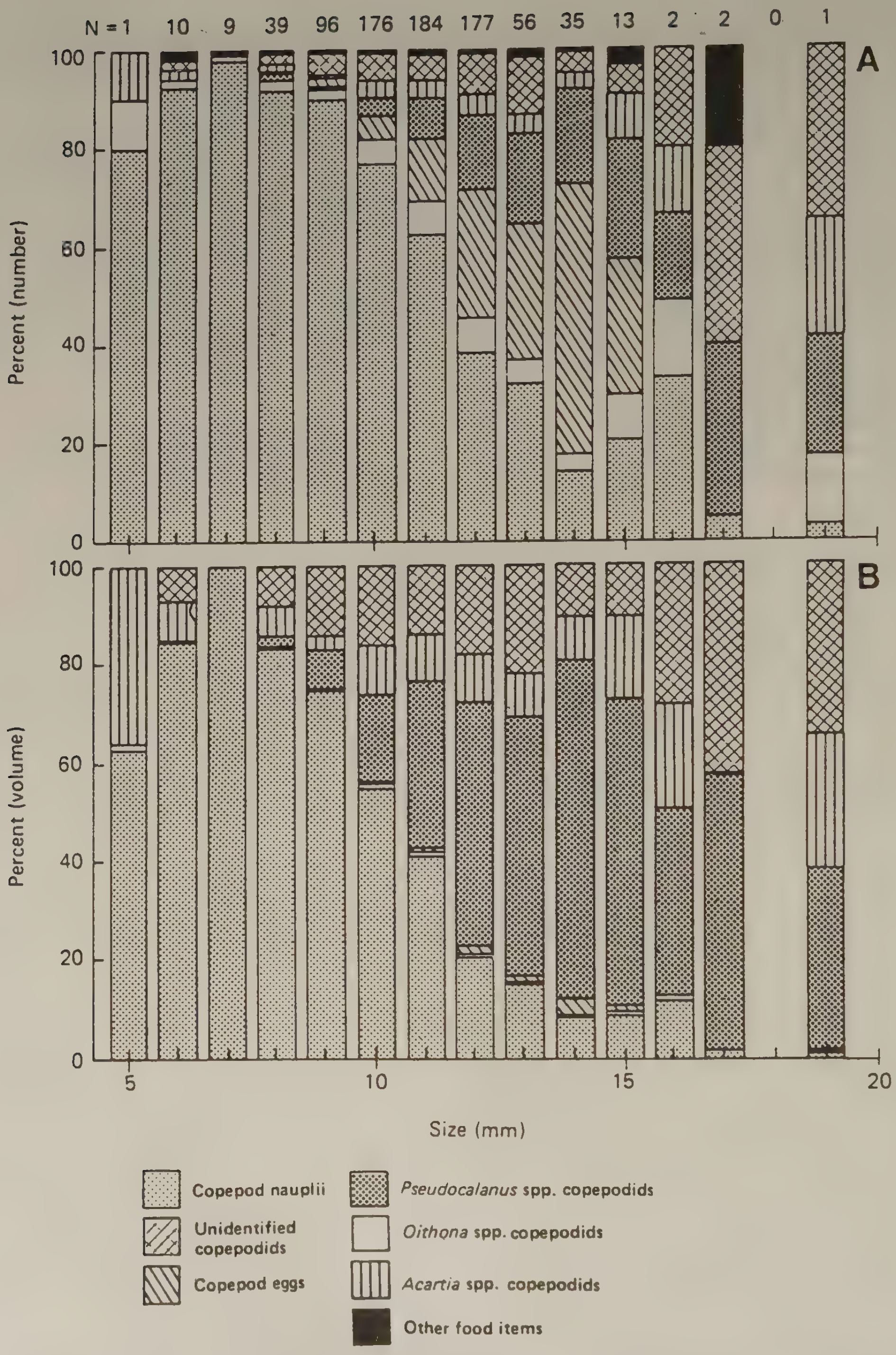

FIGURE 10.—Gut contents of walleye pollock larvae by 1 mm length intervals (5-20 mm) from northern Gulf of Alaska, May 1983. A—percent number; B—percent volume.

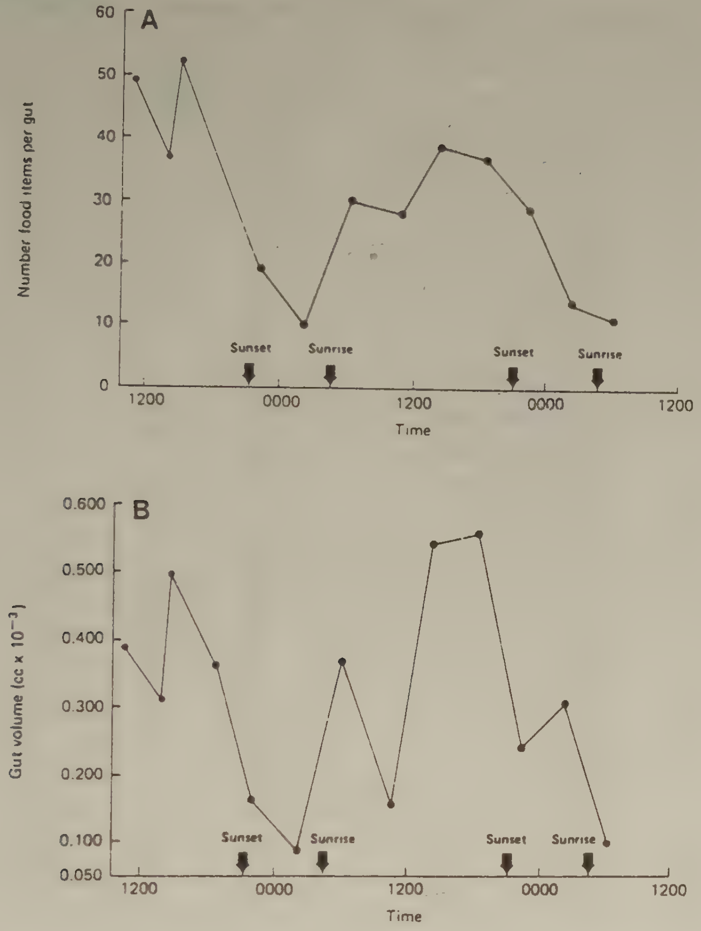

FIGURE 11.—Numbers of prey (A) and gut fullness (B) of walleye pollock larvae by time of day and depth from the vertical distribution stations, May 1983.

fied from samples taken with the 253 μm mesh net (Table 4). *Pseudocalanus* spp. were generally the most abundant taxon. Abundances of *Pseudocalanus* females ranged from 11 m^{-3} to a peak of 1,398 m^{-3} at 1515 h on the first day at a depth of 47 m. The overall mean abundance of *Pseudocalanus* females was 224 m^{-3}. These females comprised between 9 and 23% of the total zooplankton at all depth strata both during the daylight and darkness (Fig. 12). The highest percent contribution by this stage (22-23%) was during daylight hours at the two deepest strata. Peak abundances usually occurred at depth strata below 25 m. Copepodid stages of *Pseudocalanus* also reached a peak of 1,890 m^{-3} at the same station. These copepodids contributed the greatest percentage (21-33%) of the total zooplankton at all depths and times. There were no obvious patterns associated with depth or time of day in either abundance or percent composition of the total zooplankton.

Oithona spp. were abundant in the samples even though they were not collected quantitatively in the 253 μm mesh net. The peak abundance observed was 1,323 m^{-3}. *Oithona* spp. were most abundant in the surface stratum comprising 18% of the total zooplankton during the day versus <10% of the zooplankton at deeper strata during the day and at all depths during the night (Fig. 12). *Acartia* spp., *Neocalanus* spp., and *Calanus* spp. were the only other abundant copepods. The *Neocalanus* spp. and *Calanus* spp. in-

TABLE 4.—Species composition of zooplankton samples from the vertical distribution stations.

Taxon				
Number (See Fig. 11)	Name	Maximum No./10 m^3	Minimum No./10 m^3	Mean No./10 m^3
1	*Pseudocalanus* spp. adult female	13,981	118	2,245
2	*Pseudocalanus* spp. adult male	4,711	0	567
3	*Pseudocalanus* spp. copepodids 1-5	18,915	46	3,592
4	*Neocalanus* spp. and *Calanus* spp.	12,163	0	1,545
5	*Oithona* spp.	13,234	0	1,167
6	*Acartia* spp.	2,476	101	794
7	*Centropages* spp.	380	0	50
8	*Metridia* spp.	—	0	—
9	*Eucalanus bungii*	192	0	7
10	*Paracalanus* sp.	46	0	5
11	*Clausocalanus* sp.	25	0	1
12	*Tortanus* spp.	7	0	—
13	Unidentified calanoid	201	0	9
14	Euphausiid furcilia	3,431	0	511
15	Euphausiid calyptopsis	97	0	7
16	Euphausiid crytopsis	—	0	—
17	*Thysanoessa inermis* furcilia	1,307	0	517
18	*T. inermis* calyptopsis	—	0	—
19	*T. inermis* crytopsis	97	0	5
20	Euphausiid juveniles	—	0	—
21	*T. inermis* juvenile	73	0	5
22	Chaetognatha	592	0	94
23	Appendicularia	1,088	0	290
24	Hyperidae	183	0	31
25	Gastropoda	484	0	62
26	Decapoda	262	0	24
27	Balanidae	253	0	39
28	Gammaridae	7	0	—
29	*Evadne* spp.	97	0	3
30	*Limacina* spp.	1,569	0	364
31	Pontellidae	19	0	—
32	Thecosomata	255	0	21
33	Brachyura	292	0	34
34	Gymnocomata	38	0	1
35	Echinodermata	1,511	0	117
36	Hydrozoa	311	0	18
37	Pelecypoda	28	0	1
38	Medusa	14	0	—
39	Siphonophore	8	0	—

cluded *N. plumchrus*, *C. pacificus*, and *C. marshallae*. Together these species contributed between 13 and 25% of the total zooplankton (Fig. 12).

Euphausiids were the only other abundant group of zooplankters; furcillae were the most abundant stage. The abundance of furcillae was generally <200 m^{-3}; however, at 1047 h on 29 May, the numbers of furcillae exceeded 1,300 m^{-3}.

Age and Growth

Ages were determined for 109 walleye pollock larvae, including 40 individuals collected from Station 37 within the area of highest larval abundance and 69 specimens from four stations well removed from this area. Standard lengths ranged from 6.0 to 14.6 mm and mean increment counts (days since hatching) ranged from 7 to 45.5 (Table 5). The average growth rate varied from 0.12 to 0.25 mm/day among the five stations (Table 5). When compared pairwise with growth rates from all other stations, growth rates from all stations located outside the dense patch, ex-

TABLE 5.—Average growth rates, statistics on the linear regression, comparison lengths, and ages of larval walleye pollock used in growth analysis from five areas in the Shelikof Strait. Station 37 is in the area of highest larval density (Fig. 1).

Station	Y-intercept (mm)	*b*-growth (mm d^{-1})	r^2	*N*	No. of fish aged	Length range (mm)	Age range (days)
37	3.7	0.24	0.82	40	40	6.8-13.1	12-42
53	4.2	0.23	0.81	20	20	7.6-13.0	20-41
9	3.5	0.25	0.81	20	20	6.0-14.6	7-43
6	4.7	0.18	0.61	20	20	6.6-12.3	10.6-42.2
12	6.6	0.12	0.90	9	9	8.1-12.6	14-45.5

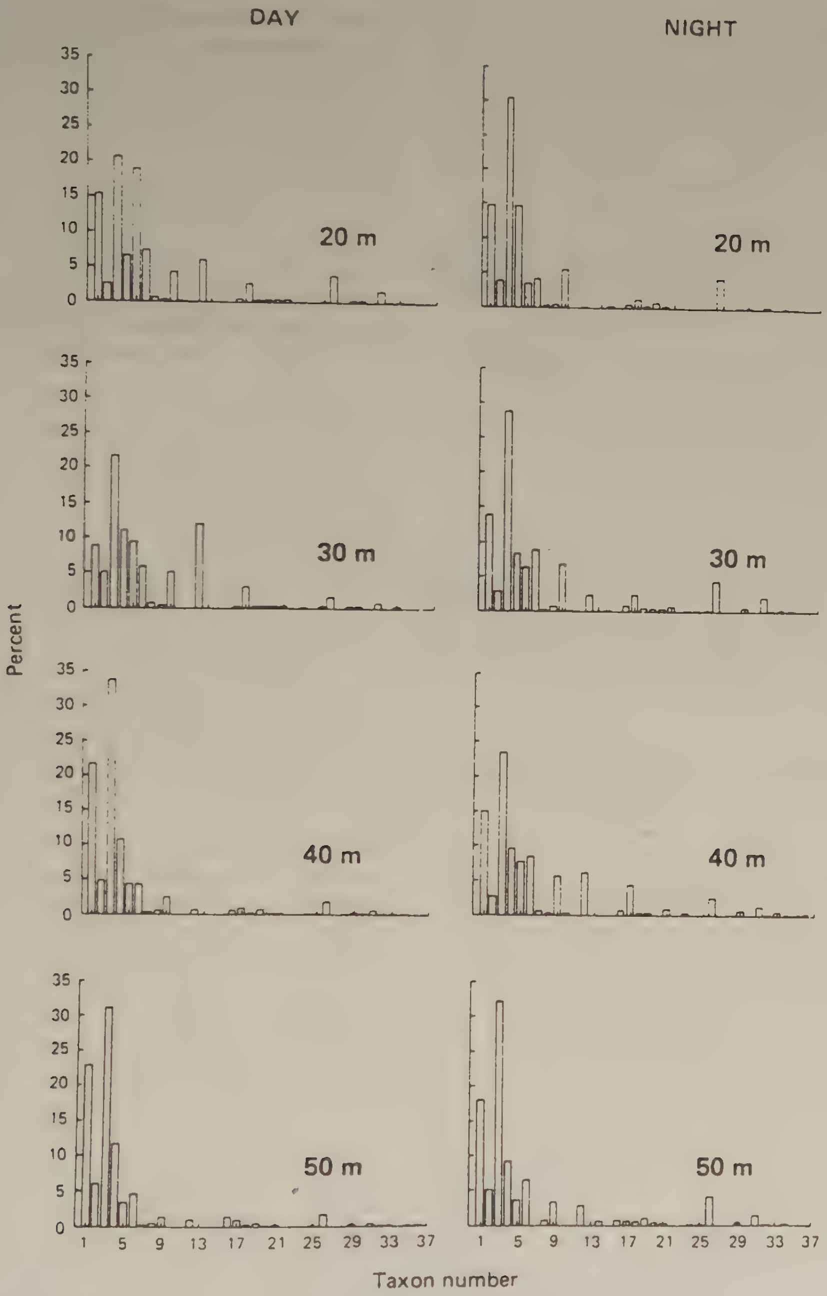

FIGURE 12.—Zooplankton distribution (percent total zooplankton) for day and night by depth from the vertical distribution stations, May 1983. Taxon numbers: 1: *Pseudocalanus* spp., adult female; 2: *Pseudocalanus* spp., adult male; 3: *Pseudocalanus* spp., copepodids 1-5; 4: *Neocalanus* spp. and *Calanus* spp.; 5: *Oithona* spp.; 6: *Acartia* spp.; 7: *Centropages* spp.; 8: *Metridia* spp.; 9: *Eucalanus bungii;* 10: *Paracalanus* sp.; 11: *Clausocalanus* sp.; 12: *Tortanus* spp.; 13: Unidentified calanoid; 14: Euphausiid furcilia; 15: Euphausiid calyptopsis; 16: Euphausiid crytopsis; 17: *Thysanoessa inermis* furcilia; 18: *T. inermis* calyptopsis; 19: *T. inermis* crytopsis; 20: Euphausiid juveniles; 21: *T. inermis* juvenile; 22: Chaetognatha; 23: Appendicularia; 24: Hyperidae; 25: Gastropoda; 26: Decapoda; 27: Balanidae; 28: Gammaridae; 29: *Evadne* spp.; 30: *Limacina* spp.; 31: Pontellidae; 32: Thecosomata; 33: Brachyura; 34: Gymnosomata; 35: Echinodermata; 36: Hydrozoa; and 37: Pelecypoda.

cept Station 12, were not statistically different from growth measured within the dense patch (Station 37). Larvae collected at adjacent Stations 6 and 12, located to the northeast of the densest area (Fig. 2), exhibited the lowest growth rates and were not statistically different from each other.

Estimated age-at-length data from all stations were combined to describe early growth in walleye pollock from the Shelikof Strait region as follows:

$$SL = 4.29 + 0.21 \text{ (age, d)} \qquad n = 109,\ r^2 = 0.75$$

where SL = standard length (Fig. 13). This relationship suggests a mean growth rate of 0.21 mm/day and an intercept of 4.29 mm, which corresponds with the known size of newly hatched larvae (Walline 1983; Nishimura and Yamada 1984).

The distribution of dates of hatching was estimated by back-calculating from the ages determined for larval walleye pollock in the Shelikof Strait. The median birthdates from all stations were similar and thus all 109 samples were combined (Fig. 14). The hatching period ranged from early April to mid-May with a mode in the last

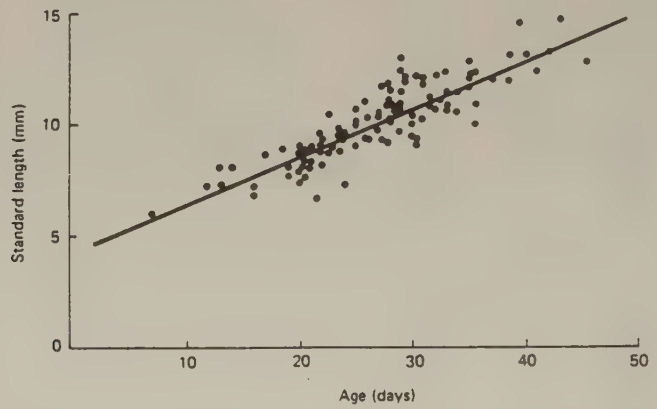

FIGURE 13.—Estimated age at length, fitted with linear regression, for all walleye pollock larvae analyzed from the northern Gulf of Alaska, May 1983.

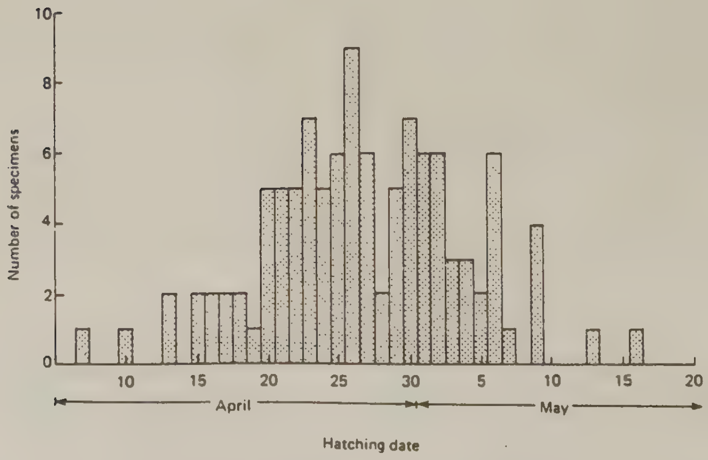

FIGURE 14.—Distribution of hatching dates for walleye pollock determined by back-calculation using age and date of collection.

week of April. Incubation time for walleye pollock eggs held at 5°-6°C in the laboratory is estimated to be 14 days (Haynes and Ignell 1983; Nakatani and Maeda 1984; Nishimura and Yamada 1984); spawning of walleye pollock occurs primarily in late March and early April in Shelikof Strait (Dunn et al. fn. 5), supporting our estimated hatching dates distribution.

DISCUSSION

Relative Abundance of Eggs and Larvae

Neuston collections in spring in the northern Gulf of Alaska have been reported only for 1978, mainly over the shelf, south and east of Kodiak Island, a month earlier than the present study (Kendall and Dunn 1985). Eggs of *Theragra chalcogramma* were most abundant; the rest of the identified eggs were of several pleuronectids. The greater abundance of *T. chalcogramma* in relation to the pleuronectids in the earlier cruise, when compared with the present data (Fig. 5), probably reflects the seasonal difference in spawning times. Pleuronectids spawn mainly in late spring and early summer in the Gulf of Alaska while *T. chalcogramma* is mainly a late winter-early spring spawner (Kendall and Dunn 1985).

Eggs have been reported from bongo catches from three other cruises in the northern Gulf of Alaska in May (Bates and Clark 1983[10]; Kendall and Dunn 1985); eggs of pleuronectids and those of *T. chalcogramma* were most abundant. However, the rank order of abundance of the various pleuronectids varied considerably among the cruises. Usually eggs of *Glyptocephalus zachirus*, *Hippoglossoides elassodon*, and *Microstomus pacificus* were among the five most abundant taxa.

Among larvae in the neuston tows during the present study, mainly spring spawning taxa (e.g., *Ammodytes hexapterus*, *Bathymaster* spp., *T. chalcogramma*) were represented; whereas larvae of fall-winter spawning taxa (e.g., three hexagrammids, and *Hemilepidotus* spp. [Irish lords]) were abundant during the earlier cruise (Kendall and Dunn 1985).

In bongo catches during other May cruises in the area, larvae of *T. chalcogramma*, *Hippoglossoides elassodon*, *Bathymaster* spp., and *A. hexapterus* have always occurred frequently, as in the present study (Bates and Clark fn. 9; Kendall and Dunn 1985).

Distribution of Walleye Pollock Eggs

The few eggs collected during the present study represented a very late part of the spawning, which occurs in Shelikof Strait mainly in early April (Dunn et al. fn. 5) (Fig. 1). Recently hatched larvae (<5 mm SL), which were collected during our survey (Fig. 2), also indicate prolonged spawning but probably at a low level after mid-April. The eggs we found were mainly over the deep waters at the southwest end of Shelikof Strait, and it would be expected that they were also farther to the northeast. This is the same area of occurrence of eggs during the height of spawning (Dunn et al. fn. 5), indicating that the adults spawn mainly in Shelikof Strait throughout this period, although individual spawning fish probably migrate in and out of the area.

Comparisons of Distribution of Walleye Pollock Larvae

In 1981, several sequential cruises to Shelikof Strait mapped a large concentration of walleye pollock eggs in early April; and in late April and again in mid-May, a concentration of larvae was found progressively further to the southwest of the area where the eggs had been (Bates and Clark fn. 10) (Fig. 1). The size of the larvae in the concentration increased between the cruises.

Sampling in 1981 and 1982 for walleye pollock larvae was at the same area and time (24-28 May) as the present study (Dunn et. al. fn. 5). Comparisons of distribution, abundance, and size of the larvae among these 3 years reveal remarkable differences (Table 6). Spawning time in 1981, based on ages of eggs caught in early April, and presence of newly hatched larvae in late April, centered around 5-8 April. In 1983, based on birthdate distributions presented here, modal spawning time was also in the second week of April. Sampling in subsequent years has shown a remarkable consistency in spawning place and time (Kendall unpubl. data). By 24-28 May the patch of larvae in 1981 and 1983 had drifted to the same area, just north of Sutwik Island (Figs.

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[10] Bates, R. D., and J. Clark. 1983. Ichthyoplankton off Kodiak Island and the Alaska Peninsula during spring 1981. U.S. Dep. Commer., Natl. Mar. Fish. Serv., NOAA, NWAFC Proc. Rep. 83-09, 105 p.

TABLE 6.—Concentrations and lengths of pollock larvae collected 24-28 May 1981, 1982, and 1983 in the patch resulting from the Shelikof Strait spawning (1981 and 1982 data from Dunn et al. text fn. 5).

Year	Cruise	Date (May)	Stations	Larvae m^{-2}	Lengths (mm SL)	
					Mean	SD
1981	4MF81	24	73, 74	2,318	7.36	1.11
	3SH81	25	225	1,285 (mean = 2,040)	7.77	1.18
1982	2DA82	24-28	108, 115, 117, 123, 124, 126	14-38 (mean = 23)	7.74	1.10
1983	1CH83	24, 28	31, 32, 36, 37, 63	104-214 (mean = 151)	11.23	1.65

1, 2). However, the abundance of larvae in 1981 was about 2,000 m^{-2} while in 1983 it was only about 150 m^{-2}. Mean length in 1981 was about 7.5 mm while in 1983 it was 11.2 mm. Since the spawning dates were the same, this would indicate a much slower growth rate (about 0.09 mm d^{-1}) in 1981 than in 1983 (0.21 mm d^{-1}). In 1982 there were fewer larvae (20 m^{-2}) and they were distributed further southwest than in the other 2 years (Dunn et al. fn. 5). These larvae were not different in length from those in 1981 (7.7 mm). The position of the larvae in 1982 suggests a much faster drift than in 1981 and 1983.

Although most of the spawning occurs in the deep trench (>200 m) in Shelikof Strait, the larvae are in the upper part of the water column. Southwest of Shelikof Strait the trench runs south between the Semidi Islands and Chirikof Island (Fig. 2). Early larvae drift in the Alaska Coastal Current which flows southwest, parallel to the Alaska Peninsula (Schumacher and Reed 1980). At the time of our surveys in May 1981 and 1983, larvae had drifted to the area between Sutwik Island and the Semidi Islands. In 1982 they were further to the southwest in water over the deeper trough and the continental shelf.

Vertical Distribution of Walleye Pollock Larvae

Vertical distribution of walleye pollock larvae has been addressed in detail in several other studies (Kamba 1977; Cooney et al. 1978; Walline 1981[11]; Dagg et al. 1984). Although the areas of study, procedures, and gear have varied, a consistent pattern of diel-vertical distribution emerges from these studies and is supported by the present study. Haryu (1980) summarized his and earlier work by stating "larvae inhabit the mid-layer rather than the surface layer and perform diurnal vertical migration in search of food." Most larvae have been found between 10 and 60 m, and within this depth range, some larvae generally move to shallower depths at night. Vertical movement is not pronounced in any of the studies but is evident by comparing proportions of larvae at various sampling depths at different times of day. In general it appears that larvae <15 mm are most concentrated vertically at 10-15 m at twilight, both in the evening and morning. During nighttime and daytime the larvae are more dispersed vertically, and during daytime their distribution is deeper than at night. Samples confined to day and night periods do not show the crepuscular nature of the distribution. This pattern is seen in the present study but is less pronounced than in some others, possibly because we conducted our sampling only in the vertical range of high concentration. Larvae larger than about 15 mm appear able to avoid plankton nets to some extent, particularly during daytime. The available data, however, suggest that these larger larvae remain concentrated in a shallow depth stratum (5-15 m) except at night when they are more dispersed vertically and may rise closer to the surface (Walline fn. 11).

Fish larvae of most other species that have been studied also migrate upward in the water column at night (Kendall and Naplin 1981). Some species undergo a much more pronounced vertical migration than is apparent with walleye pollock larvae and may cross much greater temperature gradients than observed here. Similar to walleye pollock, larvae of other fish species are visual feeders, and their vertical movements are probably associated with a diel feeding periodicity. Walleye pollock larvae may move to shallower depths at night to allow more feeding in reduced light. They then may spread downward in the water column during daytime in response to increased light penetration and the distribution of their prey. Too little is known about predation on fish larvae to assess the importance of vertical movements on predator avoidance (see Incze et al. 1984).

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[11] Walline, P. D. 1981. Hatching dates of walleye pollock (*Theragra chalcogramma*) and vertical distribution of ichthyoplankton from the eastern Bering Sea, June-July 1979. U.S. Dep. Commer., Natl. Mar. Fish. Serv., NOAA, NWAFC Proc. Rep. 81-05, 12 p.

Feeding of Walleye Pollock Larvae

The diet composition of larval walleye pollock in Shelikof Strait is similar to that described for walleye pollock larvae collected in the southeastern Bering Sea (Clarke 1978) and Uchiura Bay, Hokkaido, Japan (Kamba 1977). Copepod nauplii and copepodids of *Pseudocalanus* spp. were the dominant food items in the guts of 6-20 mm larvae in all these studies. As in this study, copepod eggs were also abundant food items. It is difficult in any of these studies to judge if the eggs were captured as individual food items or along with adult female copepods.

Feeding by larvae in the Gulf of Alaska is highest during daylight hours, as observed in other studies (Kamba 1977; Clarke 1978). Clarke (1978) reported that the few collections made at sunrise had larvae with the lowest feeding incidences. Kamba (1977) also reported that the lowest feeding incidences and the lowest abundance of food in the gut occurred near sunrise.

The high densities of larvae in the Shelikof Strait seem to have little effect on their food habits. *Oithona* spp. are abundant in the Bering Sea, Gulf of Alaska, and Uchiura Bay, Japan, and are intermediate in size between *Pseudocalanus* spp. copepodids and copepod nauplii. *Oithona* are an important component of the diet of pollock larvae in the Bering Sea, accounting for more than 25% of the total number of food items for larvae between 11.8 and 17.7 mm (Clarke 1978), but are rare in guts of larvae collected near Hokkaido (Kamba 1977), and represent <16% of the food items for all size groups in the present study. Kamba (1977) cited the low incidence of occurrence of this food item in larvae collected in Uchiura Bay as evidence of selective feeding by walleye pollock larvae.

The zooplankton species composition in the oceanic and outer shelf regions of the Bering Sea (Cooney and Coyle 1981; Smith and Vidal 1984) is similar to that described for the northern Gulf of Alaska and Ocean Station P (Le Brasseur 1965; Damkaer 1977; Fulton 1983; Miller et al. 1984). The Shelikof Strait species composition is similar to these areas. Our zooplankton sampling did not include copepod nauplii so we cannot assess their abundance. The size distribution of copepod nauplii ingested, however, indicates that *Pseudocalanus* spp. and *Oithona* spp. are the probable sources of the copepod nauplii ingested by larval walleye pollock in Shelikof Strait.

Daily production of copepod nauplii at a single station in the Bering Sea has been estimated to be 27,094 m^{-2}, of which more than 95% was *Pseudocalanus* spp. (Dagg et al. 1984). The abundance of *Pseudocalanus* females ranged from 9.9 to 258.9 m^{-3} ($\bar{x} = 87.7$). The mean abundance of *Pseudocalanus* females in Shelikof Strait was 244 m^{-3}, or 2.6 times greater than the mean abundance in the Bering Sea. Assuming the same rate of daily production, about 69,000 nauplii m^{-2} would be produced in Shelikof Strait. Mean abundance of walleye pollock larvae where Dagg et al. (1984) performed their study was 6.3 larvae m^{-2}, whereas at the diel station in Shelikof Strait the abundance was 156 m^{-2}, about 25 times greater than in the Bering Sea study. If these larvae ate nauplii at the same rate as those in the Bering Sea, 18.3 per day, they would eat about 24% of the production, as opposed to the <1% in the Bering Sea. Other factors such as the relationship between size of larvae and daily ration need to be investigated before more precise estimates of the impact of larval feeding and the possibility of food limitation can be made. It appears that enough nauplii were being produced to preclude density dependent food restrictions at the larval densities observed in the present study.

Growth of Walleye Pollock Larvae

Growth rates were similar in areas of both high and low density (Table 5, Fig. 13). It cannot be determined from our study whether density-dependent factors modified larval growth; growth variations could be produced by patchy distributions of prey. Walleye pollock larvae have been shown to grow faster in the laboratory at higher food densities (Bailey and Stehr 1986), further, where lower or constant larval densities interact with variable prey density, field studies have shown variability in growth (Govoni et al. 1985). Without knowledge of prey availability at each location, however, it is difficult to discern if high densities of prey coincide with dense patches of larvae. The relatively low growth rates found at two adjacent stations outside the patch (Stations 6, 12; Table 6) might indicate an area of less than adequate prey availability.

Growth rates for fishes can be influenced by environmental factors such as temperature, as well as availability of adequate food supplies (Boehlert and Yoklavich 1983). Within species, growth rates are usually positively correlated with temperature over the normal temperature range. Growth rate for larval walleye pollock in the Gulf of Alaska (0.21 mm d^{-1}) is considerably lower than that determined for larvae of the same size range (4-25 mm SL) collected in the southeastern Bering Sea in June-July 1979 (0.35 mm d^{-1}, Walline 1985). Water temperatures were similar in both studies (about 6°-8°C). Maximum growth determined for larvae collected in the Bering Sea in March-June 1980 while water temperature was much cooler (2°-6°C), was 0.22 mm d^{-1} (Clarke 1984). Thus differences in growth rates of larval walleye pollock in the Bering Sea could be due to differences in water temperature, food availability, or a variety of other factors which may affect growth in larvae (Bailey and Stehr 1986). Future research on growth variability in the field should take into account prey availability, temperature, and size-specific mortality rates.

SUMMARY

1. Walleye pollock in the Gulf of Alaska form an intense spawning aggregation in Shelikof Strait in late winter that produces a dense patch of planktonic eggs in early April. Larvae from this spawning can be followed as they develop and are carried by currents to the southwest during spring.
2. In late May 1981, the density of larvae in this patch (>10 m^{-3}) suggested that density-dependent effects on growth and survival might be expected. A field study of larvae in late May 1983 found maximum densities of only 1 larva m^{-3}, and investigated growth and vertical distribution, and feeding in the patch.
3. The larvae were concentrated vertically between about 15 and 50 m, and tended to be in the upper part of this range during night and early morning, whereas they were deeper during the afternoon and evening.
4. Larvae <10 mm fed primarily on copepod nauplii, with copepodids becoming more important in larvae up to 20 mm. Copepodids of *Pseudocalanus* spp. made up a large fraction of the diet of larvae >10 mm. Most feeding occurred during daylight.
5. The copepods *Pseudocalanus* spp., *Neocalanus* spp., *Calanus* spp., *Oithona* spp., and *Acartia* spp. dominated the net zooplankton samples (253 μm mesh net).
6. Growth, based on otolith increments counted on 109 larvae (6.0-14.6 mm) was linear (0.21 mm/day, intercept = 4.29 mm, $r^2 = 0.75$). Growth rates in the area of high abundance were generally not significantly different from those elsewhere.
7. While at the larval densities observed in 1981, density-dependent effects are possible, at the lower densities we observed in 1983 no such effects were expected or indicated in growth rates or diet. Future studies should include direct measurement of copepod naupliar production rates in the areas inhabited by the larvae.

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Assessment of Pacific Skipjack Tuna (*Katsuwonus pelamis*) Resources by Estimating Standing Stock and Components of Population Turnover from Tagging Data

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Kleiber, P., A. W. Argue, and R. E. Kearney. 1987. Assessment of Pacific skipjack tuna (*Katsuwonus pelamis*) resources by estimating standing stock and components of population turnover from tagging data. Can. J. Fish. Aquat. Sci. 44: 1122–1134.

More than 140 000 tagged skipjack tuna (*Katsuwonus pelamis*) were released during 3 yr over a large portion of the central and western Pacific. Tag returns exceeded 6000. We developed a set of tag attrition models to analyze tag release and return data and catch and effort statistics for the study area. We used these models to assess the status of the skipjack resource in the whole study area and within subdivisions thereof. Total standing stock was estimated at 3 million metric tons (Mt), (95% confidence range 2.5–3.7 Mt). Overall attrition rate (including losses to natural mortality, fishing mortality and emigration) was $0.17 \cdot mo^{-1}$ ($0.15-0.20 \cdot mo^{-1}$). Total throughput was estimated at $6.2\ Mt \cdot yr^{-1}$ ($5.5-7.1\ Mt \cdot yr^{-1}$) compared with catch of $<0.3\ Mt \cdot yr^{-1}$. Overall harvest ratio was 0.04. Harvest ratios for seven subareas for which detailed catch and effort statistics were available ranged from 0.02 to 0.46; only one exceeded 0.17. Low harvest ratios over most of the study area during the period tags were at large imply a potential for increased skipjack catches in many subareas and in the whole study area.

Plus de 140 000 bonites à ventre rayé (*Katsuwonus pelamis*) marquées ont été relâchées dans une zone couvrant une grande partie du centre et de l'ouest du Pacifique au cours d'une période de 3 ans. On a pu récupérer plus de 6 000 étiquettes. Les auteurs ont élaboré une série de modèles d'attrition des étiquettes pour l'analyse des données sur l'étiquetage et le retour des étiquettes et des statistiques de prises et d'effort de pêche dans la zone étudiée. Les modèles ont servi à évaluer l'état de la ressource en bonites dans l'ensemble et les subdivisions de la zone d'étude. Le stock présent a été estimé à 3 millions de tonnes métriques (Mt) (niveau de confiance à 95 % de 2,5–3,7 Mt). Le taux d'attrition total (comprenant les pertes par mortalité naturelle, pêche et émigration) a été estimé à $0{,}17 \cdot mo^{-1}$ ($0{,}15-0{,}20 \cdot mo^{-1}$). La productivité totale a été estimée à $6{,}2\ Mt \cdot an^{-1}$ ($5{,}5-7{,}1\ Mt \cdot an^{-1}$) pour des prises inférieures à $0{,}3\ Mt \cdot an^{-1}$. Le rapport de récolte total était de 0,04. Les rapports de récolte de sept sous-zones pour lesquelles on disposait de statistiques détaillées sur les prises et l'effort de pêche se situaient entre 0,02 et 0,46 et un seul était supérieur à 0,17. Les faibles rapports de récolte pour la plus grande partie de la zone étudiée au cours de la période pendant laquelle les poissons marqués étaient en haute mer supposent une possibilité d'accroître les prises de bonites dans bon nombre de sous-zones de même que dans l'ensemble de la zone d'étude.

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Annual skipjack tuna (*Katsuwonus pelamis*) catches from the area of the South Pacific Commission increased rapidly from less than 5000 metric tons (t) in the early 1960's to approximately 220 000 t in the early 1980's. Skipjack are a short-lived, fast growing, highly fecund species distributed throughout all tropical and subtropical ocean waters. Their lifestyle is apparently quite suitable for supporting a high harvest rate. Nevertheless, with increased catches, many countries in the region became concerned that interactions among surface fisheries might be sizeable and that increased yields might not be sustainable. The Skipjack Survey and Assessment Programme was undertaken by the Commission to assess the status of the skipjack resource and its ability to support this increased fishing pressure. Tagging was adopted as the principal stock assessment technique (Anonymous 1975). Between October 1977 and August 1980 the Skipjack Programme tagged and released approximately 140 000 skipjack throughout and beyond the area of the South Pacific Commission (Fig. 1). Over 6000 of these tagged fish were recaptured and reported to the Commission.

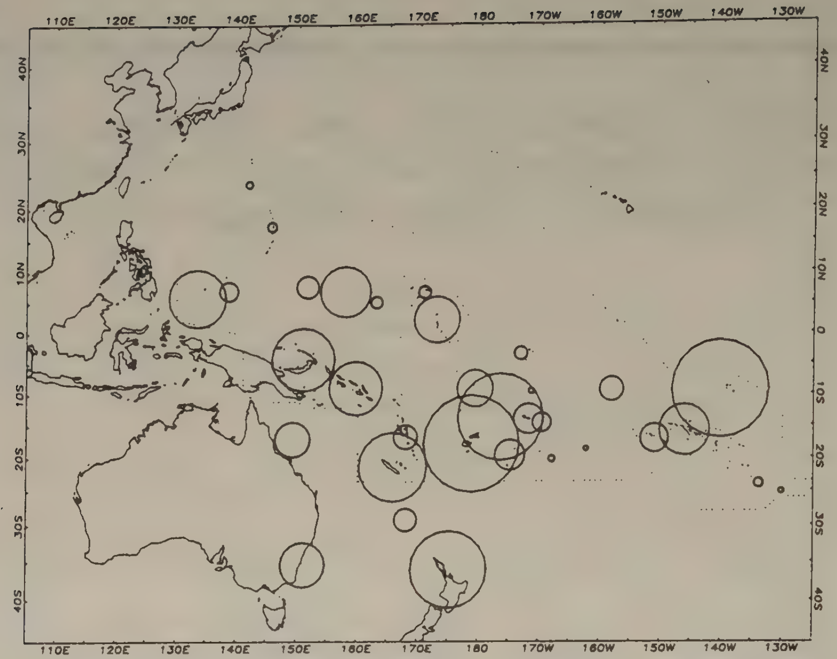

FIG. 1. Distribution of tag releases (circles) and boundaries of the South Pacific Commission Region (dotted line). The circles are centered on each subarea in which tags were released. The areas of the circles are proportional to the number of tagged skipjack released.

We present an analysis of tag release and recovery data for the purposes of assessing the standing stock of skipjack, rate of renewal (turnover) of the skipjack resource, and current levels of fishing pressure on the skipjack resource in the region as a whole and in the waters of individual countries and territories for which detailed catch and fishing effort data were available. For this purpose we developed a set of closely related analytical models which, using tagging data and catch and effort statistics, gives estimates and confidence limits for various parameters useful in defining the status of a population that is supporting a fishery. Some of these parameters are familiar: standing stock, natural mortality, and fishing mortality. Others are not so familiar but are useful in the context of this widely distributed and mobile species. We define these as follows.

Attrition: rate of loss of standing stock expressed as proportion of standing stock. It encompasses all loss factors including natural mortality, fishing mortality, emigration, and growth out of vulnerability to the fishery.

Throughput: product of attrition and standing stock; a measure of the passage of biomass through the stock. It encompasses death, emigration, and growth out of the vulnerable size class. Under steady-state conditions, it is also the in situ productivity plus immigration of vulnerable-sized individuals.

Harvest ratio: ratio of catch rate to throughput (equivalent to the ratio of fishing mortality to attrition). If fishing mortality is small relative to the population turnover, i.e. the harvest ratio is low, it is likely that fishing is having little impact on the population.

Tagging and Tag Recovery Methods

Tagging was carried out over a period of 3 yr in three 10-mo cruises each using one chartered Japanese pole-and-line vessel. The itinerary of the tagging cruises covered the whole study area, which includes the area of the South Pacific Commission and some adjacent waters where skipjack were known to be abundant (Kearney 1982b). The number of tags released in each area was not uniform (Fig. 1) because tagging success depended on fishing conditions, which were quite variable in space and time.

Skipjack were captured by pole-and-line fishing. The fish were poled onto tagging cradles where they were measured and tagged with plastic dart tags according to the technique described by Kearney and Gillett (1982). Fishermen on local and foreign-based vessels and workers at processing facilities were the primary sources of returned tags. Locally based fisheries within the study area were the pole-and-line operations in Papua New Guinea, Solomon Islands, Fiji and Palau, the *alia* fishery in Western Samoa, the *bonitier* fishery in the Society Islands of French Polynesia, and the purse-seine fishery in New Zealand. Information on local fisheries is contained in the final reports to the individual countries by the Skipjack Programme (e.g. Kearney 1982a; Argue and Kearney 1982, 1983; Gillett and Kearney 1983; Kleiber and Kearney 1983). Foreign fleets taking significant quantities of skipjack at the time most tags were at large were the long-range Japanese pole-and-line fleet and steadily increasing Japanese and United States purse-seine fleets.

Rewards were given and lotteries conducted to encourage return of tags (Kearney 1982b). It was possible to check efficiency of part of the tag return system with a tag-plant experiment in which 131 fish from the holds of purse-seiners were tagged and replaced in the holds by New Zealand Ministry of Agriculture and Fisheries personnel during the 1980–81 New

Zealand fishing season.

To investigate tag shedding and mortality due to tagging, a double tagging experiment was carried out in the waters of Fiji in 1980, during which 5399 double tagged skipjack were released, interspersed with 5626 single tagged fish (Skipjack Programme 1981). A further experiment was conducted with skipjack held at a research facility of the United States National Marine Fisheries Service at Kewalo Basin, Honolulu. Sixteen captive skipjack were tagged with Skipjack Programme tags and were observed for 7 wk along with 14 untagged controls (R. E. Kearney, unpubl.).

Analytical Methods

We assessed population parameters by analyzing plots of tag return rate (number of tags returned per unit time) against time at large. The tag return rate is expected to decrease with time because tag density in the fished populations should decline due to a variety of factors (e.g. mortality, emigration, tag shedding). The analyses described in this report were performed with a set of models in which tag return rates are predicted as a function of time from release and in which variations in exploitation are taken into account. The choice of model depends on which parameters are to be estimated and on whether catch data or effort data are used.

Derivation of Models

Immediate mortality and shedding have been defined as type 1 losses (Beverton and Holt 1957, p. 201; Bayliff and Mobrand 1972). These losses reduce the effective number of tagged fish at large at time zero. Thus if N_0 fish are tagged and if α is type 1 survival, then the effective number of tagged fish at the start is αN_0.

Following type 1 losses, a number of other factors reduce the population of tagged fish. Factors that affect all fish include natural mortality, emigration, fishing mortality, and growth out of vulnerability to the fishery. In addition, the population of tagged fish can undergo what is called type 2 or long-term loss by tag shedding and extra mortality due to carrying a tag. If, following type 1 losses, all attrition factors operate such that the tagged population decreases exponentially, then the number of tagged fish at large as a function of time, t, following tagging is

$$(1) \quad N = \alpha N_0 e^{-(Z+\psi)t}$$

where Z = total attrition rate for a group of untagged fish (time^{-1}) and ψ = additional attrition for tagged fish (time^{-1}). The rate at which usable tags are returned is given by

$$(2) \quad \frac{\partial r}{\partial t} = \beta F N = \alpha N_0 e^{-(Z+\psi)t}$$

where r = cumulative number of usable tag returns, F = fishing mortality (time^{-1}), and β = proportion of recaptured tags that are actually returned with usable recapture information. (Not all tag returns could be used in the analysis because some had unknown or imprecisely known times of recapture.)

We assume that ψ and β are constant during the time that tags are recovered. We also assume that Z is constant even though F, which is a component of Z, is likely to vary considerably with changes in effort expended by the fishery. For $Z \gg F$, this assumption in not bad, and later we will relax this assumption.

Defining F_i to be the average fishing mortality during the ith time unit following tagging and integrating Equation 2 under the assumption of constant attrition gives

$$(3) \quad r_i = \frac{\alpha\beta N_0 F_i}{(Z+\psi)} e^{-i(Z+\psi)} \left[e^{(Z+\psi)} - 1\right]$$

where r_i is the number of usable tag returns in time unit i. Equation 3 is a general model from which particular models were derived based on the following considerations.

The unknown fishing mortalities, F_i, can be approximated by

$$(4) \quad F_i \simeq q f_i \simeq \frac{c_i}{P}$$

where c_i = catch in biomass units in time unit i, P = standing stock in biomass units (assumed constant in time), q = catchability coefficient, or fraction of the standing stock harvested by one unit of fishing effort, and measured in inverse units of fishing effort (assumed constant in time), and f_i = units of fishing effort in time unit i.

Thus, either catch data or effort data can be used depending on which term in Equation 4 is substituted for F_i in Equation 3. Whether catch data or effort data are used influences the parameter estimates. Therefore, parameters that were estimated both ways are differentiated by a subscript, c, for parameters in models using catch data and a subscript, f, for parameters in models using effort data.

To complete the derivation of particular models, the following equations were substituted into the general model. The throughput (biomass per unit time) is given by

$$(5) \quad T = Z_c P.$$

Fishing mortality is not treated as constant over all time intervals, but a measure of the average fishing mortality can be obtained. If we have an average catch rate, $\bar{c}$, or an average effort rate, $\bar{f}$, then the average fishing mortality is given by

$$(6) \quad F_c = \frac{\bar{c}}{P}; \; F_f = q\bar{f}.$$

The harvest ratio (unitless) is then given by

$$(7) \quad H_c = \frac{F_c}{Z_c}; \; H_f = \frac{F_f}{Z_f}.$$

The resulting set of models is detailed in Table 1 wherein each equation, except for the last, has two parameters relevant to stock assessment which are confounded with α, β, and ψ, which we will call nuisance parameters.

The last model in Table 1 is an exception. All others allow the fishing mortality to vary with time, but contain the paradoxical assumption that the attrition rate is constant. When catch is used, this inconsistency is difficult to correct because standing stock should vary if the attrition varies. The model would therefore need to incorporate input and output of untagged fish with an attendant list of further assumptions.

However, when effort is used, it is logically consistent to allow to varying attrition rate and still assume a constant catchability. Defining M = attrition rate of untagged fish exclusive of fishing mortality (time^{-1}), we can substitute $M + F + \psi$ for Z in Equation 2. Then substituting qf_i for F and integrating leads to the last equation in Table 1. In this model the quantity $\alpha\beta$ is no longer confounded with other parameters. Therefore in theory this model could be used to estimate $\alpha\beta$. Note that the effort must vary for this to work because if f_i is constant, this

TABLE 1. Set of models used for estimating population parameters.

Parameters	Model
Z_c P	$r_i = \frac{\alpha\beta N_0 c_i}{P(Z_c + \psi)} e^{-i(Z_c+\psi)} \left[e^{(Z_c+\psi)} - 1\right]$
Z_f q	$r_i = \frac{\alpha\beta N_0 q f_i}{(Z_f + \psi)} e^{-i(Z_f+\psi)} \left[e^{(Z_f+\psi)} - 1\right]$
Z_c T	$r_i = \frac{\alpha\beta N_0 Z_c c_i}{T(Z_c + \psi)} e^{-i(Z_c+\psi)} \left[e^{(Z_c+\psi)} - 1\right]$
Z_c F_c	$r_i = \frac{\alpha\beta N_0 F_c c_i}{\bar{c}(Z_c + \psi)} e^{-i(Z_c+\psi)} \left[e^{(Z_c+\psi)} - 1\right]$
Z_f F_f	$r_i = \frac{\alpha\beta N_0 F_f f_i}{\bar{f}(Z_f + \psi)} e^{-i(Z_f+\psi)} \left[e^{(Z_f+\psi)} - 1\right]$
Z_c H_c	$r_i = \frac{\alpha\beta N_0 Z_c H_c c_i}{\bar{c}(Z_c + \psi)} e^{-i(Z_c+\psi)} \left[e^{(Z_c+\psi)} - 1\right]$
Z_f H_f	$r_i = \frac{\alpha\beta N_0 Z_f H_f f_i}{\bar{f}(Z_f + \psi)} e^{-i(Z_f+\psi)} \left[e^{(Z_f+\psi)} - 1\right]$
$\alpha\beta$ M q	$r_i = \frac{\alpha\beta N_0 q f_i}{(M + q f_i + \psi)} e^{-\left[iM + q \sum_{j=1}^{i} f_j + i\psi\right]} \left[e^{(M + q f_i + \psi)} - 1\right]$

	Desired parameters
P	standing stock
T	throughput
q	catchability
Z_c, Z_f	total attrition
F_c, F_f	fishing mortality
M	natural attrition
H_c, H_f	harvest ratio
	Nuisance parameters
α	type 1 tag retention and survivorship
β	proportion of recaptured tags that are reported and useful
ψ	type 2 tag slippage and mortality
	Input data
r_i	tag returns in time period i
c_i	catch in time period i
f_i	effort in time period i
$\bar{c}$	average catch per time period
$\bar{f}$	average effort per time period
N_0	number of tags released

model reverts to a two-parameter form.

Fitting the Models

Parameters were estimated by fitting the models given in Table 1 to the tag return results, with input of catch or effort data and input of independent estimates of $\alpha\beta N_0$ and ψ. Fitting was conducted iteratively with either the generalized Marquardt algorithm (Conway et al. 1970) or the simplex algorithm of Nelder and Mead (1965). The varying attrition model could be fitted with all three parameters being adjusted or with one or two of the parameters fixed.

Because finding a tagged fish among many untagged fish is a rare event, we presumed that the statistical distribution of tag counts is approximately the Poisson distribution. We therefore used a square root transformation (Sokal and Rohlf 1969, p. 384).

Goodness-of-fit, G, was measured by the proportion of the total variance in the observed data accounted for by the model, i.e.

$$(8) \quad G = 1 - \frac{S_{\min}}{(n-k)\sigma_T^2}$$

where $S_{\min}$ is the minimum residual sum of squares, n is the number of data points used in the analysis, k is the number of parameters estimated, and σ_T^2 is the variance of the transformed input data.

Confidence Limits

When fitting two-parameter models, the boundary of the joint confidence region of the two parameters corresponds to a contour line on the sum-of-squares surface at which the residual sum of squares is equal to a critical value defined by

$$(9) \quad S_{\text{crit}} = S_{\min}\left[1 + \frac{k}{(n-k)} F_{0.05(k,n-k)}\right]$$

where $F_{0.05(k,n-k)}$ is the critical value of the F-distribution at probability level 0.05 with k and $n-k$ degrees of freedom and where k is the number of data points used in the analysis (Conway et al. 1970). A numerical searching algorithm was devised to trace the contour on the sum-of-squares surface. With the varying attrition model, when three parameters were fitted, it was necessary to trace a critical sum-of-squares shell in three dimensions with the critical sum-of-squares given by Equation 9 with $k = 3$. Confidence intervals for individual parameters were obtained from the extremes of the joint 95% confidence region.

Note that except for the actual observed tag return data, uncertainties in input data are ignored in this method of calculating confidence intervals.

Determining Values for β

Estimating β is complicated by the fact that tagged fish can be found in a variety of ways. For the purpose of this analysis we assumed two discovery modes: by fishermen and by personnel of shore-based processing facilities. Recaptured tags can be broken into usable returns from fishermen, unusable returns from fishermen, tags found by fishermen but not returned, and tags missed by fishermen. The latter category can be further broken into usable returns from shore, unusable returns from shore, tags found ashore but not returned, and tags not found at all. An expression β can be derived as follows. Let u_f, u_s = number of usable returns from fishermen and from shore, v_f, v_s = number of unusable returns from fishermen and from shore, ζ_f = tags returned as a proportion of tags found by fishermen, and ζ_s = tags returned as a proportion of tags missed by fishermen (i.e. as proportion of all tags that came ashore, whether found or not). The β factor is the ratio of the number of usable returns to the total number of recaptures and is given by

$$(10)\quad \beta = \frac{u_f + u_s}{\dfrac{u_f + v_f}{\zeta_f} + \dfrac{u_s + v_s}{\zeta_s}}.$$

Assumptions of the Models

In addition to the usual assumptions that tagged and untagged fish are equally vulnerable to fishing gear, a series of assumptions was made in deriving the set of analytical models. Simulations were conducted to investigate the consequences to the parameter estimates of violating some of these assumptions (P. Kleiber, A. W. Argue, J. R. Sibert, and R. Farman, unpubl.).

Temporal distribution of tag releases

One assumption is that all tags are released at time zero rather than throughout the first time interval. This is correct for the aggregate data set but not so for most subarea data. The simulation results showed that the models are insensitive to this problem as long as tag returns are available for more than a few time intervals.

Constant parameter values

A principal assumption is that there is little variation in parameter values during the tagging experiment. To use the catch-based models, the population and the attrition rate should be constant; to use the effort-based models, the catchability and the attrition rate should be constant. A subsidiary assumption, for all but the variable attrition model, is that variations in fishing mortality are small relative to the total attrition rate. Simulation showed that the models are robust to large cyclical variations from steady state. In this case the estimates are close to the average values of the varying parameters. If there are large one-way trends, the models are less robust, and the standing stock and catchability estimates tend to reflect the starting values more than the averages.

A result detrimental to effective fishery management would occur if the harvest ratio was so underestimated that the fishery appeared capable of sustaining increased fishing pressure when in fact it could not. In the simulation exercise, the scenarios under which this could happen involved a drastic downward trend in the population, particularly when this was in response to a sharp decrease in recruitment or a sharp increase in mortality. A sharp decrease in recruitment or increase in mortality by a factor of 2 caused underestimation of the harvest ratio by less than a factor of 1.4. Thus, large departures from steady state cause smaller underestimates of the harvest ratio.

Parameters that apply to individual fish, such as attrition rate, are also assumed to be the same for all fish, though we might expect that such parameters would vary as a function of size or age. In a preliminary analysis we found little evidence for an effect of fish size on total attrition rate (see below).

Territory covered by tagging experiment

An implicit assumption in the derivation of the models is that the stock, of which P is a measure, is a clearly defined entity. However, the effective boundary of the stock which the tagged fish represent is not so clearly defined when the area of operation of a fishery is surrounded by unfished areas and when the fish in the fished area can exchange with fish in the unfished area. In such a case, the territory occupied by a cohort of tagged fish can be expected to expand with time. However, the number of tagged fish simultaneously diminishes due to attrition, which thereby limits the duration of the experiment. The effective size of the territory covered by the tagging experiment therefore depends on the relative rates of migratory expansion and attrition. A simulation of this situation resulted in an estimated stock size corresponding to the population occupying a zone approximately twice the area of the fished zone.

Data Used in Analyses

Table 2 gives the tag return data and other input data used in the analyses. Two data sets were organized differently from the others. These are the data for the whole study area, i.e. aggregate data, and for the Trust Territory and Guam subarea. For these we combined the returns from many tag release episodes according to time at large (elapsed time between release and recapture) without regard to the actual dates of release and recapture. Thus the returns in any months-at-large category were not necessarily all contemporaneous. We did this because detailed catch and effort statistics were not available for all of the release episodes which occurrred at many times throughout the 3 yr of the release phase of the tagging experiment and at many places throughout these large areas. This lack of fishery statistics precluded analyzing the release episodes separately. No fundamental change to the models was necessary except that a constant average catch rate had to be assumed because of lack of better data and because the tags, being noncontemporaneous, could not all be associated with the same historical series of catch rates.

The tag data for all subareas other than the Trust Territory and Guam refer to releases and recaptures during specific date spans, 10-d periods for New Zealand and months for other areas.

In Table 2, the t columns identify either the months-at-large category or the specific date span of recapture. The r_i columns give the number of usable recaptures in the territory in question. The few recaptures by the tagging vessel were excluded for all data sets because the fishing effort of this vessel was, for the most part, identical to the places and times of tag release. Returns with unknown dates of recapture were also excluded. If an imperfectly known recapture date could be ascertained to fall within a range of dates such that the extent of the range was less than half the time from release to the midpoint of the recapture range, then the return was accepted and the recapture date taken to be the midpoint of the range. Otherwise the return was rejected. For some individual subareas, the returns were additionally filtered (see below).

The c_i columns in Table 2 give the tons of skipjack caught, and the f_i columns, if present, give the effort in boat days, or purse-seine sets in the case of New Zealand. Except for the Trust Territory and Guam, catch and effort for the first recapture period in each subarea data set were prorated to adjust for timing of tag release during the initial period.

Average monthly catch, $\bar{c}$, and effort, $\bar{f}$, were used in some models. The averages were calculated over the period of time included in the data set. Months with zero catch and effort were included in the average. Catch and effort in individual months could be considerably different from the average, particularly for the highly seasonal New Zealand fishery. Catch and effort were averaged for December–March in New Zealand.

In several cases, the first one or two recapture periods in a

TABLE 2. Tag return and other data used to estimate population parameters. Includes aggregate and subarea data sets.

Aggregate data αβ = 0.60 $\bar{c}$ = 19 000			Trust Territory and Guam αβ = 0.68 $\bar{c}$ = 4900			New Zealand αβ = 0.37 $\bar{c}$ = 2300 $\bar{f}$ = 150				Papua New Guinea αβ = 0.68 $\bar{c}$ = 2000 $\bar{f}$ = 670				Solomon Islands (1977) αβ = 0.64 $\bar{c}$ = 1200 $\bar{f}$ = 340				Fiji αβ = 0.80 $\bar{c}$ = 350 $\bar{f}$ = 120				Society Islands French Polynesia αβ = 0.82 $\bar{c}$ = 100			Gilbert Group Kiribati αβ = 0.82 $\bar{c}$ = 20		
t	r_i	c_i	t	r_i	c_i	t	r_i	c_i	f_i	t	r_i	c_i	f_i	t	r_i	c_i	f_i	t	r_i	c_i	f_i	t	r_i	c_i	t	r_i	c_i
N_u = 140 000			N_u = 8887			N_u = 2678				N_u = 6009				N_u = 1709				N_u = 11 646				N_u = 823			N_u = 4403		
a1	2820	19 000	1	45	4900	790221	2	336	37	a7905	20	379	114	7711	17	754	317	a8004	594	185	76	7812	0	60	7807	26	22.6
2	506	19 000	2	14	4900	790301	223	2396	120	a7906	391	2153	598	7712	10	365	397	a8005	183	65	86	7901	1	56	7808	159	49.5
3	379	19 000	3	10	4900	790311	7	148	18	7907	208	2972	1035	7801	0	15	73	8006	6	76	42	7902	4	64	7809	82	63.5
4	261	19 000	4	43	4900	790321	30	215	24	7908	100	2492	913	7803	0	15	34	8007	11	116	33	7903	4	91	7810	78	76.3
5	198	19 000	5	35	4900	790401	1	3	1	7909	58	1840	899	7804	3	941	460	8008	19	90	49	7904	1	110	7902	0	0.8
6	120	19 000	6	16	4900	791121	0	25	7	7910	27	654	614	7805	5	888	465	8009	2	99	20	7905	3	170	7903	0	3.8
7	115	19 000	7	14	4900	791201	0	15	7	7911	5	811	706	7806	1	1526	515	8010	2	79	21	7906	2	130	7904	1	9.4
8	93	19 000	8	16	4900	791221	0	35	6	7912	3	286	212	7807	5	1973	551	8011	2	106	45	7907	0	94	7905	0	8.3
9	94	19 000	9	5	4900	800101	5	1319	94	8003	1	609	440	7808	3	1587	512	8012	11	229	41	7908	0	89	7906	0	26.8
10	114	19 000	10	2	4900	800111	0	2100	87	8004	5	1956	802	7809	4	2304	517	8101	27	737	198	7909	0	48	7907	0	8.8
11	142	19 000	11	0	4900	800121	1	1186	86	8005	1	2243	985	7810	7	2317	497	8102	42	862	161	7910	0	62	7908	0	12.1
12	106	19 000	12	4	4900	800201	3	1986	135	8006	2	2860	1005	7811	5	2915	514	8103	35	953	193	7911	0	100	7909	0	6.8
13	72	19 000	13	0	4900	800211	1	142	18	8007	3	2878	1068	7812	5	2723	518	8104	8	605	150						
14	62	19 000	14	0	4900	800221	0	219	33	8008	7	5514	1100	7901	1	1106	223	8105	12	536	138	N_u = 896					
15	75	19 000	15	3	4900					8009	5	3982	988	7904	2	1438	305	8106	10	418	132						
16	42	19 000	16	3	4900	N_u = 6298				8010	0	3697	850	7905	0	1788	485	8107	5	387	140	a7901	0	7			
17	17	19 000	17	1	4900					8011	0	3055	831					8108	1	76	23	7902	2	64			
18	24	19 000	18	1	4900	790301	280	1917	96	8012	0	1800	553	Solomon Islands				8110	3	77	33	7903	1	91			
19	16	19 000	19	2	4900	790311	8	148	18	8101	0	222	99	(1980)				8111	1	143	82	7904	0	110			
20	23	19 000	20	2	4900	790321	48	215	24	8103	0	1814	447	αβ = 0.54				8112	2	298	147	7905	0	170			
21	13	19 000	21	0	4900	790401	0	3	1	8104	0	4675	918	$\bar{c}$ = 2200				8201	0	600	224	7906	0	130			
22	8	19 000	22	0	4900	791121	0	25	7	8105	0	3085	977	$\bar{f}$ = 490				8202	1	686	226	7907	0	94			
23	10	19 000	23	0	4900	791201	0	15	7	8106	0	3340	962					8203	1	696	241	7908	0	89			
24	11	19 000	24	0	4900	791221	0	35	6	8107	1	3421	1077	t	r_i	c_i	f_i	8204	0	485	231	7909	0	48			
25	3	19 000				800101	5	1319	94	8108	1	2100	964					8205	0	589	275	7910	0	62			
26	6	19 000				800111	3	2100	87	8109	0	1660	805	N_u = 2012				8206	0	285	168	7911	0	100			
27	8	19 000				800121	6	1186	86	8110	0	1435	626					8207	0	118	81	7912	1	54			
28	7	19 000				800201	6	1986	135	8111	0	426	185	8006	9	354	179	8208	0	42	31	8001	0	190			
29	2	19 000				800211	1	142	18	8112	0	77	42	8007	28	2550	558					8002	0	130			
30	0	19 000				800221	0	219	33					8008	25	2778	554					8003	0	83			
31	1	19 000				800301	1	1191	76					8009	9	2770	574					8004	0	82			
32	1	19 000				800311	0	493	36					8010	8	3244	566					8005	0	160			
33	1	19 000				800321	1	113	19					8011	20	3313	566					8006	0	97			
34	1	19 000				800501	0	18	5					8012	16	2774	594					8007	1	78			
35	0	19 000				800521	0	49	5					8101	18	1531	463					8008	0	32			
36	1	19 000				800601	2	35	9					8104	5	1210	258					8009	0	55			
37	0	19 000				800611	0	12	2					8105	5	1881	560					8010	0	150			
38	0	19 000												8106	11	2934	614					8011	0	130			
39	0	19 000												8107	4	2796	628					8012	0	180			
40	0	19 000												8108	6	3474	640										
41	0	19 000												8109	2	2631	639										
														8110	0	2087	630										
														8111	0	2131	632										
														8112	1	1231	415										

data set were disregarded in the analysis. In Table 2 the rows corresponding to these are preceded by an "a." The early returns in any tagging experiment can easily be anomalous because of inadequate mixing of tagged fish in the tagged population. In the present analysis, early returns were disregarded if there was good reason to assume a problem with mixing in the first recapture period(s), and if doing so significantly improved the ability of the model to fit the data.

For each subarea other than the Trust Territory and Guam, releases and recoveries were selected to make the analysis relevant to a local fishery. Releases made outside the area of the local fishery were eliminated as was one release of fish of a substantially different size range than were caught in the local fishery. Tags recovered outside the subarea of release were not considered. Details of tag selection are presented in individual reports prepared for each subarea (Kearney 1982a; Argue and Kearney 1982, 1983; Gillett and Kearney 1983; Kleiber and Kearney 1983; Tuna Programme 1984a, 1984b).

Results and Discussion

Estimation of Nuisance Parameters

Considerable effort was expended to maintain high standards in the tagging procedure (Kearney and Gillett 1982) to maximize α, in the tag return system (Kearney 1982b) to maximize β, and in the quality of the tags themselves to minimize ψ. To analyze the results, however, it was necessary to estimate values for these nuisance parameters.

Estimates of $\alpha\beta$ *with the variable attrition model*

The variable attrition model (last equation in Table 1) was fitted to the five data sets containing effort in Table 2. N_o was set to the values given in Table 2, and the parameters M, q, and $\alpha\beta$ were adjusted by the fitting procedure. In three cases the process converged to impossible values (negative M or $\alpha\beta$ greater than 1), and in two cases possible values resulted. Investigation of the three-dimensional confidence regions for the latter two cases (Fig. 2 and 3) revealed that $\alpha\beta$ was very ill-defined by the analysis. The 95% confidence range (approximately 0.05$-$1.0) covers most of the possible range (0$-$1).

Estimation of β

Estimation of β using Equation 10 requires the factors ζ_f and ζ_s. A range of values for ζ_f can be obtained from the double tagging results in Fiji. Using the approach of Bayliff and Mobrand (1972), an estimate of 0.997 (95% confidence range 0.82$-$1.0) was obtained for the quantity $\rho d_f \zeta_f$, where ρ is the short-term (type 1) tag retention (1 minus tag shedding rate) and where d_f is the proportion of recaptured tags that are discovered by fishermen (Tuna Programme, unpubl. analyses). This range also applies to ρ, d_f, and ζ_f individually because all three quantities can only be in the range (0$-$1).

In a tag-plant experiment designed to measure ζ_s, 25% of the planted tags were returned, all from shore-based processing facilities, principally in Pago Pago. This experiment was conducted more than 1 yr after most of the recoveries from the regular tagging program were obtained from shore facilities. Thus, it is possible that the low recovery of planted tags reflects a more recent problem in the tag recovery system, or a problem specific to seine-caught fish from New Zealand processed in Pago Pago. Unfortunately, tag-plant experiments were not done on pole-and-line caught fish or on fish destined for other processing facilities. It is also possible that tags placed in dead fish are more easily lost than tags placed in live fish. Taking the tag-plant results at face value, ζ_s could have been as low as 0.25. However, ζ_s might very well have been higher for Pago Pago and other processing facilities during the time that tagged fish from live releases were passing through these facilities. Worst and best case values of 0.25 and 1.0 were assumed for ζ_s.

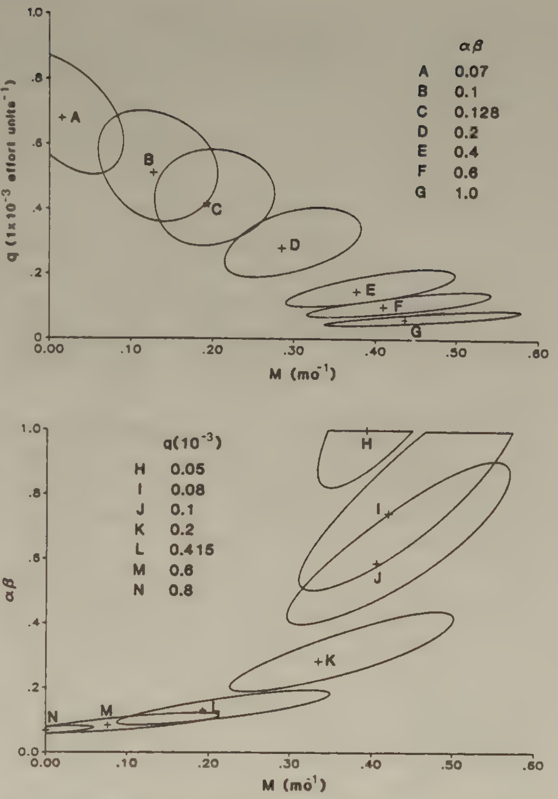

FIG. 2. Confidence regions for estimates of the three parameters of the variable attrition model using the Papua New Guinea data set. In the upper plot, slices through the confidence region at various levels of $\alpha\beta$ are shown. The $\alpha\beta$ axis extends downward from the plane of the page. In the lower plot the figure is rotated forward about the M-axis so that the q-axis rises upward from the plane of the page. Slices at various levels of q are shown. In the upper plot, the crosses give the best-fitting q and M values with $\alpha\beta$ fixed at each level, and in the lower plot the crosses give the best-fitting $\alpha\beta$ and M values with q fixed at each level. The star in each plot gives the best-fitting point for the three-parameter fit.

Assuming the ranges given above for ζ_f and ζ_s, worst and best case values of β were calculated by Equation 10 and are given in Table 3.

Estimation of α

The parameter α depends on type 1 mortality and type 1 tag shedding. As shown above, the type 1 tag shedding rate, $1 - \rho$, must be low. Type 1 tagging mortality is more difficult to determine. However, high tag return rates (>50%) have been observed in the eastern Pacific (Anonymous 1978). This strongly suggests that the combination of type 1 tagging mortality and tag shedding was low. This conclusion is further

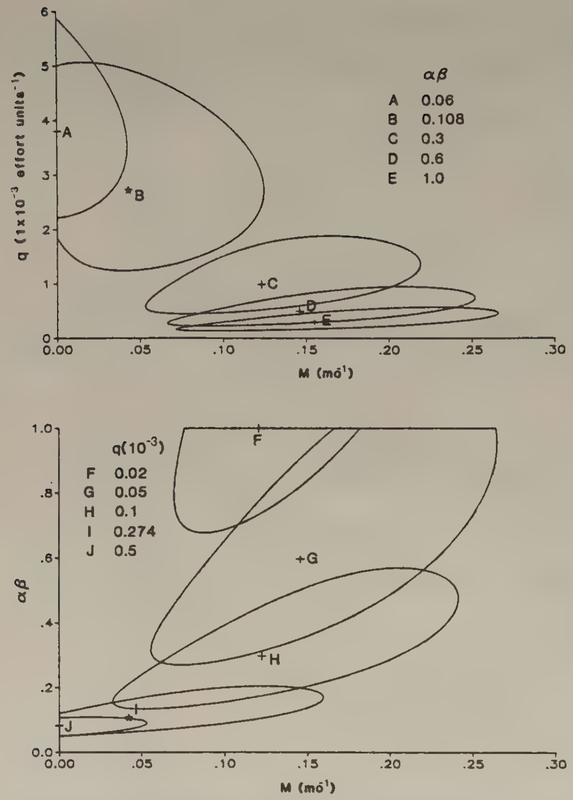

FIG. 3. Confidence regions for estimates of the three parameters of the variable attrition model using the 1980 Solomon Islands data set. In other respects, this figure is similar to Fig. 2.

TABLE 3. Worst and best case values of β are calculated from Equation 10 using worst and best case assumptions about ζ (0.82 and 1.0 for ζ_f; 0.25 and 1.0 for ζ_s).

Data set	Where found	Tag returns: Useable u	Tag returns: Reject v	β: Worst case	β: Best case
Aggregate	Fishermen	4641	125	0.47	0.87
	Shore	711	706		
Trust Territory and Guam	Fishermen	190	9	0.58	0.94
	Shore	26	6		
New Zealand	Fishermen	231	12	0.19	0.64
	Shore	403	352		
Papua New Guinea	Fishermen	838	7	0.62	0.90
	Shore	0	82		
Solomon Islands (1977)	Fishermen	65	1	0.55	0.88
	Shore	3	8		
Solomon Islands (1980)	Fishermen	167	6	0.43	0.77
	Shore	0	45		
Fiji	Fishermen	977	23	0.80	0.98
	Shore	1	0		
Society Islands	Fishermen	20	0	0.82	1.0
	Shore	0	0		
Gilbert Group	Fishermen	346	0	0.82	1.0
	Shore	0	0		

TABLE 4. Distribution of tag returns among subareas for three classes of size at release. The total returns are not necessarily the same as the totals of returns in Table 2 because in this case, tags were selected with regard to the existence of accurate length measurement at release and accurate time of recapture, but without regard to other selection criteria involved in assembling the data sets in Table 2.

Data set	Fork length: <45 cm	Fork length: 45–55 cm	Fork length: >55 cm	Total tag returns
Aggregate	634	3536	630	4800
Fiji	139	1380	114	1633
Solomon Islands	157	290	55	502
Papua New Guinea	14	573	311	898
Palau	204	52	51	307
Ponape	1	95	44	140
New Zealand	100	536	8	644
Wallis and Futuna	3	67	6	76
Tuvalu	1	21	6	28
Gilbert Group	3	354	8	365

supported by an experiment with captive skipjack in which no significant difference in mortality between tagged and untagged fish was observed (R. E. Kearney unpubl.).

In the absence of further quantitative information, a figure of 10% has been assumed here for the type 1 losses, i.e. a value of 0.9 for α.

Values of αβ *used in subsequent analyses*

The values of αβ used as input to the analytical model are given at the head of each data set in Table 2. These were derived from an assumed value of 0.9 for α and a value for β midway between the worst and best case values given in Table 3.

Type 2 tag loss, ψ

The parameter ψ can include type 2 shedding and also type 2 mortality. Type 2 shedding estimated from double tagging was $0.0073 \cdot \mathrm{mo}^{-1}$ (Skipjack Programme 1981). Type 2 mortality is not so readily estimated, but the double tagging results suggest that it is a minor factor. Except for fish smaller than 45 cm, the proportion returned of the double-tagged skipjack was not significantly less than that of single-tagged skipjack released at the same time (Skipjack Programme 1981). The difference noted for small fish could have resulted from type 1 (affecting α) or type 2 (affecting ψ) losses. We looked for and did not find any influence of size on total attrition, $Z + \psi$ (see next section), as would be expected if there was significant, size-dependent, type 2 mortality. This suggests that the reduction in returns for the small double-tagged fish was predominantly a type 1 phenomenon. In any case, these small fish accounted for less than 15% of the returns considered in this report. Type 2 mortality was therefore assumed to be zero, and the value of ψ for all data sets was taken to be the estimate of type 2 tag shedding.

Effect of Size at Release on Attrition

To test for the effect of size at release on attrition rates, the

TABLE 5. Estimates of tag attrition (mo^{-1}) with 95% confidence intervals for three classes of size at release. Results are given for the aggregate data set and for subareas with 20 or more returns in more than one size class. One data set, WTG, is the sum of returns for Wallis and Futuna, Tuvalu, and the Gilbert Group.

Data set	Fork length		
	<45 cm	45−55 cm	>55 cm
Aggregate	0.17 (0.15−0.20)	0.17 (0.14−0.20)	0.27 (0.22−0.33)
Fiji	0.18 (0.10−0.32)	0.57 (0.09−0.24)	0.12 (0−0.33)
Solomon Islands	0.17 (0.11−0.26)	0.18 (0.12−0.25)	0.27 (0.17−0.42)
Papua New Guinea		0.34 (0.21−0.58)	0.63 (0.42−0.92)
Palau	0.21 (0.17−0.27)	0.15 (0.08−0.25)	0.37 (0.19−0.69)
Ponape		0.20 (0.13−0.29)	0.22 (0.06−0.48)
New Zealand	1.1 (0.9−10.4)	1.2 (0.9−10.5)	
WTG		0.24 (0.14−0.46)	0.30 (0.07−0.69)

aggregate tagging data and seven subsets of the data were broken into three categories of size at release, <45, 45−55, and >55 cm (Table 4). Six subsets consisted of subarea data with 20 or more returns in at least two of the size categories. One additional subset was made up of returns from three subareas which in combination gave 20 or more returns in two size classes.

The aggregate and six of the subsets were put into months-at-large classes in the same way as the aggregate data in Table 2. The New Zealand subset was broken into 10-d periods. Total attrition was estimated by fitting the first model in Table 1 to the data, using a constant catch rate for subarea as well as aggregate data under the assumption that the effects of changing catch rate on attrition estimates would be roughly equivalent for the different size classes.

The resulting attrition estimates (Table 5) can be used to compare size classes within a subarea or the aggregate data set, but they should not be used to compare attrition rates between countries. The only significant result is a higher attrition rate for large fish in the aggregate case. However, a large portion of the large fish were released in Papua New Guinea (Table 4) where, as we shall see (Table 6), the attrition rate was particularly high. Therefore the result for aggregate data could be a Papua New Guinea effect instead of a size effect, a conclusion that is supported by the lack of significant effect of size for individual subarea data.

Tag Attrition Curves

The decline in tag return rate with time is shown for the aggregate data set in Fig. 4. As indicated in Table 2, the value for the first month was not included in the fitting. The bump in the observed data at approximately 1 yr could be the result of seasonality in the fisheries. Most fisheries in the region have a period of higher fishing effort each year lasting from a little over 1 mo (New Zealand) to several months (Papua New Guinea). Because tags tended to be released in each subarea during these periods, it is to be expected that a surge of tag returns would coincide with increased fishing, approximately 1 yr following tagging.

The predicted values decline smoothly in Fig. 4 because we could not account for variations fishing activity in the aggregate case. When we were able to account for such variations, the predicted values decline jerkily (Fig. 5) because they reflect variations in catch, as well as the steady decline due to all the components of attrition.

Parameter Estimates from the Analytical Model

Table 6 gives goodness-of-fit and parameter estimates obtained from all but the variable attrition model. Table 7 gives the goodness-of-fit and parameter estimates obtained by fitting the variable attrition model to the data sets for which effort data were available.

The results from the variable attrition model are close in most cases to the corresponding results from the fixed attrition models. The goodness-of-fit was not improved, and the catchability estimates are likewise much the same. The last two columns in Table 7 match well except for the New Zealand results. In this case the discrepancy between variable attrition and fixed attrition models may be due to the large degree of seasonality in the New Zealand fishery, the resulting large variation in attrition being more easily accounted for by the possibility of variable attrition in the model.

The parameter estimates in Tables 6 and 7 form the basis of Skipjack Programme reports for individual subareas wherein the implications of these results to fisheries in the subareas are discussed in detail.

Reliability of the parameter estimates

The confidence limits reported in Tables 6 and 7 do not include uncertainty in the values of the nuisance parameters, and therefore, the confidence ranges in the tables are minimum estimates.

Accounting for uncertainty in ψ (the type 2 shedding rate) would directly affect the confidence ranges of attrition, and thus to a similar extent the estimates of throughput and harvest ratio. The 95% confidence range of ψ is $0.0031-0.0116 \cdot mo^{-1}$. However, given its small magnitude relative to the attrition rate, its variance is unlikely to significantly affect the confidence ranges of any of the above parameters.

Accounting for the uncertainty in the value of $\alpha\beta$ would affect the confidence ranges of all parameters except Z_c and Z_f. The range between the best and worst case estimates of β can be large (Table 3), and the assumed value of α is a guess based on little quantitative information. The confidence ranges given in Tables 6 and 7 would be larger if the uncertainty in $\alpha\beta$ had been included, which can be seen in the three-parameter confidence regions for Papua New Guinea and Solomon Islands, 1980 (Fig. 2 and 3). It is interesting to note, however, that the effect of uncertainty in $\alpha\beta$ is dependent on whether this quantity is in the upper or lower part of its possible range (0−1). Thus the confidence range of M is considerably reduced if $\alpha\beta$

TABLE 6. Results from the analytical models in Table 1 using data in Table 2. The upper figure in each cell is the best parameter estimate, and if given, the lower two figures are the 95% confidence limits. Effort data was not available for all data sets; therefore, there are some blank cells for quantities that depend on the effort value. For the New Zealand and Society Islands, data from releases in consecutive periods were used in one fitting of the model. G_c = % of variance explained by model with catch data, G_f = % of variance explained by model with effort data, P = standing stock (Mt), T = throughput (Mt·mo^{-1}), q = catchability (sets^{-1} in New Zealand, vessel-days^{-1} elsewhere), Z_c = attrition (mo^{-1}) with catch data, Z_f = attrition (mo^{-1}) with effort data, F_c = fishing mortality (mo^{-1}) with catch data, F_f = fishing mortality (mo^{-1}) with effort data, H_c = harvest ratio (dimensionless) with catch data, H_f = harvest ratio (dimensionless) with effort data.

Data set	G_c	G_f	P (10^3)	T (10^3)	q (10^{-3})	Z_c	Z_f	F_c	F_f	H_c	H_f
Aggregate	0.95		3000 2500–3700	520 460–590		0.17 0.15–0.20		0.0063 0.0051–0.0077		0.037 0.032–0.042	
Trust Territory and Guam	0.71		660 370–1310	150 100–250		0.23 0.14–0.36		0.0074 0.0038–0.0131		0.032 0.020–0.048	
New Zealand	0.91	0.85	13 10–17	5.0 3.8–7.0	1.2 0.8–1.7	0.38 0.30–0.52	0.39 0.29–0.62	0.17 0.13–0.22	0.18 0.12–0.25	0.46 0.33–0.60	0.46 0.29–0.65
Papua New Guinea	0.96	0.95	35 27–45	13 11–16	0.090 0.060–0.144	0.38 0.32–0.46	0.47 0.35–0.65	0.058 0.045–0.075	0.061 0.040–0.097	0.15 0.13–0.18	0.13 0.10–0.16
Solomon Islands (1977)	0.69	0.52	49 25–124	11 7–19	0.027 0.008–0.065	0.23 0.13–0.34	0.14 0.01–0.29	0.024 0.010–0.049	0.0092 0.0027–0.0223	0.11 0.06–0.17	0.067 0.034–0.270
Solomon Islands (1980)	0.63	0.68	89 49–185	13 9–22	0.056 0.029–0.096	0.15 0.07–0.26	0.16 0.09–0.26	0.025 0.012–0.046	0.027 0.014–0.047	0.16 0.10–0.25	0.17 0.11–0.24
Fiji	0.80	0.68	39 20–79	7.3 4.8–11.4	0.081 0.036–0.164	0.19 0.13–0.26	0.19 0.12–0.26	0.0091 0.0044–0.0174	0.0097 0.0043–0.0197	0.048 0.031–0.072	0.056 0.030–0.084
Society Islands	0.36		9.7 1.8–67.1	5.7 2.1–20.1		0.59 0.20–1.30		0.010 0.001–0.055		0.017 0.005–0.048	
Gilbert Group	0.91		1.0 0.5–2.1	0.38 0.24–0.64		0.37 0.16–0.69		0.019 0.009–0.038		0.052 0.031–0.083	

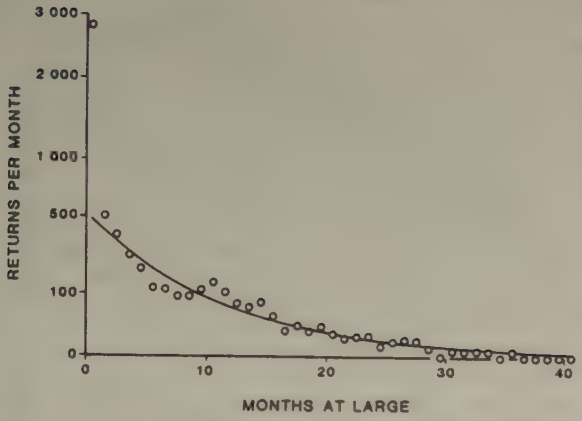

FIG. 4. Aggregate tag attrition curve. Points are the aggregate tag return rates (Table 2). The solid line gives the expected values based on the best fit of first model form in Table 1. The y-axis is a square root scale.

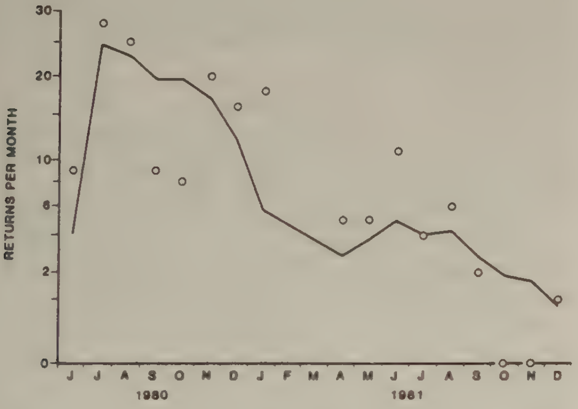

FIG. 5. Example tag attrition curve for a subarea (Solomon Islands, 1980). In other respects, this figure is similar to Fig. 4.

is known to be greater than 0.4, but more precise definition of $\alpha\beta$ within the range 0.4–1 would not narrow the confidence range of M much further (Fig. 2 and 3).

It must be stressed that the parameter values for individual subareas, and overall, apply to the time of the tagging experiment. Since that time, significant changes have occurred in several fisheries in the region. In addition, periodic major environmental events occur that presumably could affect skipjack populations in the tropical central and western Pacific waters (Wyrtki 1975; Donguy and Henin 1978).

Standing stock and throughput

The standing stock in different areas, under conditions of uniform stock density, would be proportional to the size of the area. Therefore, differences among individual country results would reflect the size of the areas covered by the different tagging experiments, which by design roughly covered the area of the locally based fisheries. Such is evident in Table 6 by comparison of P for the Gilbert Group with P for the other individual subareas. The Gilbert Group estimate is smaller than all others, and the "fishery" was a single vessel survey concentrated near a single atoll, a much smaller area than the other individual country fisheries. The aggregate estimate of P is much larger than the sum of estimates for individual subareas in Table 6 because these are only a portion of the area included in the aggregate. Between these extremes, differences among subareas are difficult to interpret, firstly because of the large overlapping confidence intervals and secondly because of the difficulty in evaluating the effective area covered by the fisheries during the tag recovery period.

TABLE 7. Results from varying attrition model with data sets containing effort values in Table 2. The parameter $\alpha\beta$ was fixed to the values given in Table 2. The format of the entries in each cell is the same as in Table 6. For comparing M with results from fixed attrition models, values of attrition minus fishing mortality ($Z_f - F_f$) from Table 6 are included in the last column of this table.

Data set	G	q (10^{-4})	M	$Z_f - F_f$
New Zealand	0.85	13 9–18	0.35 0.25–0.58	0.21
Papua New Guinea	0.95	0.88 0.60–1.30	0.41 0.31–0.55	0.41
Solomon Islands (1977)	0.51	0.26 0.08–0.64	0.13 <0.01–0.27	0.13
Solomon Islands (1980)	0.68	0.55 0.39–0.96	0.14 0.07–0.22	0.13
Fiji	0.68	0.79 0.35–1.56	0.18 0.12–0.24	0.18

Throughput, T, should be only approximately proportional to the size of the fished area, since throughput is the product of attrition and standing stock and attrition has a component due to emigration which is expected to vary inversely with the size of the fished area.

Attrition

Attrition and its components are not expected to be proportional to the area covered by the experiment. However, attrition is not necessarily independent of area because it includes a component due to dispersive movement of fish. This component tends to increase in importance with decreasing size of the area under consideration. Therefore the attrition is expected to vary inversely with area and, for large areas, approach a dispersion-free attrition rate. It is probably for this reason that the aggregate attrition estimate was lower than all but one of the individual country estimates (though only three have nonoverlapping confidence intervals).

Under the assumption of steady state, the attrition rate is also the population turnover rate. Simulation modelling showed that in a non-steady-state situation the attrition estimate would tend to reflect the average attrition over the time of the experiment. Thus if the lack of steady state is attributable to seasonal fluctuations, and tags are returned over a period of at least 1 yr, then the attrition estimate would reflect the yearly average population turnover. Furthermore, simulation showed that in nonequilibrium conditions (i.e. when the sum of inputs is different from the sum of outputs), the estimate of Z_c tends to be closer to the sum of inputs and Z_f closer to the sum of outputs. The implication is that if Z_c is larger than Z_f, then the population is increasing whereas if Z_c is less than Z_f, then the population is decreasing. The only cases in which there were appreciable differences between Z_c and Z_f were the results from the 1977 Solomon Islands data set ($Z_c > Z_f$) and from the Papua New Guinea data set ($Z_c < Z_f$). (The confidence regions given in Table 6 are not relevant in judging the significance of a difference between estimates of Z_c and Z_f when these parameters are obtained from the same data sets because there is likely to be a high positive covariance between the two estimates, which would tend to minimize the variance of the difference between them.) It may only be fortuitous that the increasing trend in P in Solomon Islands (October 1977 versus June 1980) was consistent with that predicted by the 1977 estimates of Z_c and Z_f, since the confidence intervals for the two estimates of P are large and overlapping. (In this case, where the results from two independent sets are compared, the confidence regions in Table 6 are relevant.) The trend predicted for Papua New Guinea could not be checked because there was no further tagging experiment in these waters.

The aggregate estimate of attrition is $0.17 \cdot \mathrm{mo}^{-1}$ (0.15–0.20). When fishing mortality is subtracted the remaining attrition is $0.16 \cdot \mathrm{mo}^{-1}$. Joseph and Calkins (1969) reported a comparable estimate of skipjack attrition, excluding F, of $0.14 \cdot \mathrm{mo}^{-1}$ from a tagging experiment in the northern zone of the eastern Pacific fishery. Ssentongo and Larkin (1973) gave a method for calculating attrition in exploited fish populations given the length of fish at recruitment, the mean length in the catch, and values for the parameters L_∞ and K of the von Bertalanffy growth model. For skipjack, assuming a length at recruitment of 38 cm and a mean length in the catch of 50.4 cm (the mean length of skipjack tagged by Skipjack Programme), and using values of $L_\infty = 62.5$ cm and $K = 0.17 \cdot \mathrm{mo}^{-1}$ (Sibert et al. 1983), the predicted value of attrition is $0.24 \cdot \mathrm{mo}^{-1}$, which drops to $0.23 \cdot \mathrm{mo}^{-1}$ when our estimate of F is subtracted. Pauly (1979) reported a regression equation for predicting natural mortality of a fish species given its von Bertalanffy parameter values and its mean environmental temperature. The regression equation was based on reported natural mortality estimates from a wide variety of fish families (including skipjack among several examples of scombrids). It is unclear to what extent attrition mechanisms other than natural mortality and fishing mortality are included the estimates used to derive the regression equation. Assuming the values given above for L_∞ and K and a mean water temperature of 25°C, the Pauly estimate of natural mortality for skipjack is $0.18 \cdot \mathrm{mo}^{-1}$, which is similar to our overall estimate of attrition.

Catchability

Catchability coefficients, q, for pole-and-line gear (Table 6) range from $2.7 \times 10^{-5} \cdot \text{fishing day}^{-1}$ for November 1977 tagging in Solomon Islands to $9.0 \times 10^{-5} \cdot \text{fishing day}^{-1}$ for May–June 1979 tagging in Papua New Guinea; however, all estimates have overlapping confidence intervals and little can be made of the differences among subareas. For purse-seiners in New Zealand, q is $1.2 \times 10^{-3} \cdot \text{set}^{-1}$ or $1.8 \times 10^{-3} \cdot \text{fishing day}^{-1}$ using the average of $1.5 \text{ sets} \cdot \text{fishing day}^{-1}$ for the 1979–80 and 1980–81 New Zealand fishing seasons (Argue and Kearney 1983). This catchability for purse-seiners is 28 times higher than the average for pole-and-line gear in Table 6, which probably reflects greater fishing power for purse-seiners and greater skipjack vulnerability in the coastal waters of New Zealand.

Harvest ratio

Having defined the harvest ratio and having obtained estimates thereof, it is useful to have a bench mark to show whether a given estimate is high, indicating heavy fishing pressure, or low, indicating the possibility for increased yield. The harvest ratio is analogous to the X-factor of Gulland (1971), defined such that

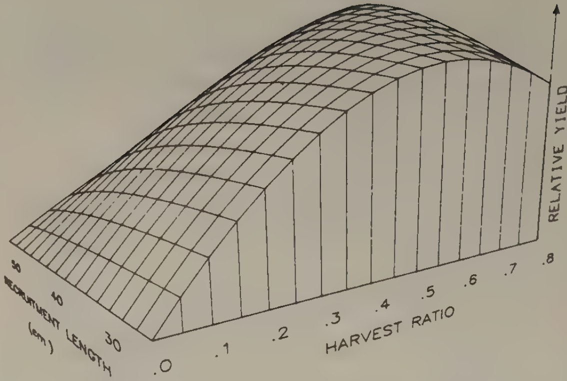

FIG. 6. Beverton-Holt yield surface. Relative yield is plotted as a function of harvest ratio and length at recruitment. Natural mortality is assumed to be $0.16 \cdot \mathrm{mo}^{-1}$. L_∞ and K of the von Bertalanffy growth model are assumed to be 62.5 cm and $0.17 \cdot \mathrm{mo}^{-1}$, respectively (Sibert et al. 1983).

$$(11) \quad Y = XT_v$$

where Y is the potential yield and T_v is the virgin turnover. On the basis of two arguments, Gulland suggested that the maximum yield from a fishery is obtained with a value of approximately 0.5 for X. One argument is based on the Schaefer model and has been shown by Francis (1974) to be unreliable. The other argument is based on the Beverton–Holt yield per recruit model wherein for a broad range of conditions, the maximum yield per recruit is obtained with a value close to 0.5 for X. Beddington and Cooke (1983) argued that for most realistic sets of parameter values, a value of X somewhat smaller than 0.5 gives maximum yield. However, if the Beverton–Holt yield is calculated for a skipjack-like fish with the values of L_∞ and K assumed above and a natural mortality of $0.16 \cdot \mathrm{mo}^{-1}$, the harvest ratio (or X) producing maximum yield is seen to be in the neighborhood of 0.5–0.7 with a size at recruitment between 36 and 40 cm (Fig. 6). It should be noted that the sustainability of yields under Gulland's second argument depends on an assumption of constant recruitment, regardless of standing stock level (Beddington and Cooke 1983). Nevertheless, a harvest ratio close to 0.5 would seem to be a good signpost for a skipjack fishery approaching full exploitation.

The estimates of harvest ratio (Table 6) tend to be lower than 0.5. For the aggregate case, the harvest ratio is low, 0.04, implying that fishing is having little impact on the skipjack resource in the study area as a whole. For subareas with well-established commercial fisheries (New Zealand, Papua New Guinea, and Solomon Islands), harvest ratios are higher, 0.15–0.46, while the other subareas, which have small or fledgling fisheries, have low harvest ratios, <0.1. Low harvest ratios for a large part of the study area imply that there is a potential for greatly increased skipjack yield, both within individual subareas and in the study area as a whole. However, recently expanded purse-seine fisheries in the vicinity of the Trust Territory, Papua New Guinea, and Solomon Islands have undoubtedly realized some of this potential.

Conclusion

The results of the analyses given in this paper provide evidence that the resource of skipjack in the study area of the Skipjack Programme is large, its rate of turnover is high, and the rate of mortality due to fishing during the study period was only a small fraction, <0.05, of the rate of turnover. This implies that skipjack catches over the whole study area could be substantially increased from those of the study period. The tag recapture and attrition models used to obtain aggregate estimates and confidence intervals for standing stock, turnover, and fishing mortality were applied to tagging data from subareas with skipjack fisheries for which catch statistics were available. Parameter estimates so derived suggest that the impact of fishing in the smaller areas is larger than the overall impact of fishing.

It should be emphasized that the results reported here apply to the time of the tagging experiment. Substantial development of purse-seining has occurred in the region since that time. This large increase in fishing effort, the large confidence intervals of parameter estimates, and the occurrence of high harvest ratios in some subareas all argue for a cautious approach in planning further development of skipjack fisheries in the central and western Pacific.

The analytical techniques used in this study are based on a set of models derived to address the situation of skipjack and of the tagging experiment conducted by the Skipjack Programme. With due attention to our discussion of assumptions, these techniques could be applied to other situations with similar salient features. The activity of the fishery can vary during the experiment, but large trends in conditions of fishery or environment during the experiment should be a warning signal. The behavior of the fish should be similar across all sizes (ages) that are tagged and should not have large trends during the experiment. These analyses should be used cautiously with long-lived fish that are exposed to the fishery for a long time, but fish like skipjack with a high turnover rate, and consequent short time in the fishery, would be good candidates.

Acknowledgements

This study was a part of the Skipjack Survey and Assessment Programme and later the Tuna and Billfish Programme of the South Pacific Commission and was funded jointly by Australia, France, Japan, New Zealand, the United Kingdom, and the United States. The success of this study depended on the hard work of the tagging vessel crew, including R. D. Gillett, J.-P. Hallier, C. P. Ellway, J. Ianelli, and D. Whyman, among many others. For counsel during the analysis of data and preparation of this report we thank J. R. Sibert, M. J. Williams, J. Wetherall, R. Allen, R. Francis, and two anonymous reviewers.

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ASSESSMENT OF INTERACTION BETWEEN NORTH PACIFIC ALBACORE, *THUNNUS ALALUNGA*, FISHERIES BY USE OF A SIMULATION MODEL

P. KLEIBER AND B. BAKER[1]

ABSTRACT

Using a simulation model of a typical year in the North Pacific albacore fisheries in the 1970s, we tested for the degree to which the activity of fleets affects the performance of other fleets. The results show that rather drastic (factor of two) changes in the activity of any of the three principal albacore fleets have only a mild effect on the catch of the other fleets. With the overall exploitation rate in the model close to the exploitation rate determined from tagging results (6%), the maximum degree of interaction was a 7.5% drop in longline catch resulting from doubling the baitboat effort. The mild degree of interaction was insensitive to exploitation rate up to approximately 10% exploitation, although interaction became more severe at higher levels of exploitation.

Fishery interaction, the effect of one fishing fleet on another, is a phenomenon of growing concern to those involved in the management and development of pelagic fisheries. This concern has arisen from the growing awareness that oceanic fishery resources are not unlimited and from the evolution of exclusive economic zones to protect local interests against large international fishing fleets. Assessing the potential for interaction between tuna fisheries in different island countries was one of the principal reasons that the South Pacific Commission conducted the Skipjack Survey and Assessment Programme (Kearney 1983). Workshops on this topic have been held during international tuna fishery meetings, and a Tuna Fisheries Interaction Programme has been proposed within the Indo-Pacific Tuna Development and Management Programme.

Because there is a multiplicity of fleets and nations involved in harvesting albacore, *Thunnus alalunga*, a tuna, in the North Pacific, there is a potential concern about interaction between these fleets. A history of North Pacific albacore fishing since the 1950s is summarized by Laurs (1983). Three principal fleets have been responsible for the catch: the Japanese baitboat, the Japanese longline, and the United States jigboat fleets (Fig. 1). In the 1970s these accounted for more than 90% (60%, 15%, and 18%, respectively) of the total catch. In recent years, Japanese gill net gear has become important, accounting for approximately 20% of the total catch from 1981 through 1983 (Fig. 1). Detailed statistics on this emerging fishery are not currently available.

Among the three principal fleets, the U.S. fleet tends to take the smallest fish, and the longline the largest, but the size distributions in the catch overlap to a large extent (Fig. 2). The geographic distribution of the fleets is indicated in Figure 3, but the overlap is overemphasized because there is seasonal separation in many cases. Nevertheless, the migratory nature of albacore makes for potentially significant interaction between fleets that are separated in time and space.

Because there have been no clear trends in catch or in catch per effort (Laurs 1983), it has been assumed that the albacore stocks have not been adversely affected by the fisheries, and such woes as the fishermen have had have not been blamed on poor status of stocks. Therefore there has been little reason for fleets to accuse one another of depleting the stocks and thus little concern about fishery interaction. To verify that sanguine view, we have estimated the degree of interaction between the three principal albacore fisheries in the North Pacific. We defined interaction to be the degree to which changes in the activity (effort) of one fleet affect the performance (catch) of another fleet. The magnitude of this kind of interaction cannot be calculated directly from fishery data, nor can controlled, real-life experiments be conducted on the grand scale necessary to address this topic. However, experiments conducted on simulation model are feasible. The results of such experiments with an

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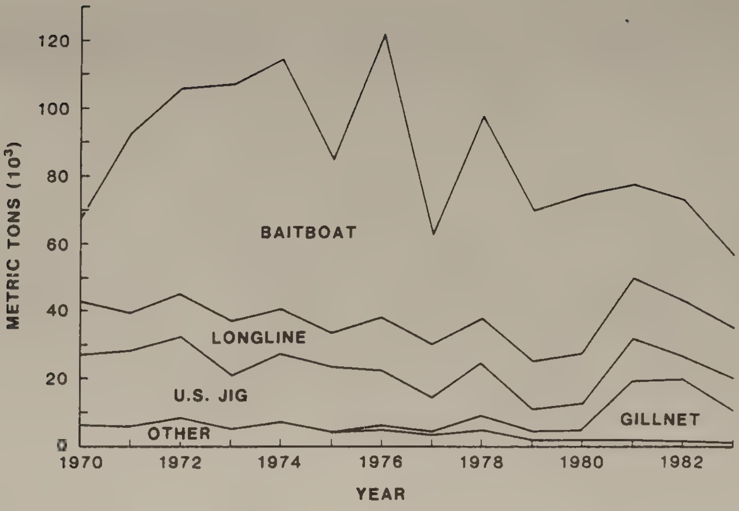

FIGURE 1.—Annual catch of albacore by gear type. [Data from Majors and Miller. 1985. Summary of the 1984 North Pacific albacore fishery data. U.S. Natl. Mar. Fish. Serv., Southwest Fish. Cent. Admin. Rep. LJ-85-14, 45 p.]

albacore simulation model are the subject of this report.

THE MODEL

We used a model that incorporates recruitment, growth, migration, natural mortality, and harvest of albacore by the Japanese baitboat fleet, the Japanese longline fleet, and the United States surface fleet (primarily jig gear). Our approach was to manipulate the effort of one fleet at a time and note the effect on the catch of the other fleets.

A full technical description of the model is given by Kleiber and Baker[2]. We discretized fish size into 5 cm length classes and the North Pacific range of albacore into nine geographic zones (Fig. 3). The basic dynamics within a size class and zone are described by the following differential equation:

$$\frac{dP_{s,z}(t)}{dt} = G_{s-1}P_{s-1,z}(t) + \sum_{\mathrm{z}} \mu_{\mathrm{z}\to z} P_{s,\mathrm{z}}(t)$$

$$- \left[M + G_s + \sum_{\mathrm{z}} \mu_{z\to \mathrm{z}}\right] P_{s,z}(t) - \sum_{g} c_{s,z,g}$$

where $c_{s,z,g} = q_{s,g}\, f_{z,g}(t)\, P_{s,z}(t)$ is the catch rate (number per unit time) by size, zone, and gear. The symbols are defined as follows:

s —index for size class
z —index for geographic zone
z —index for zone adjacent to z
g —index for gear type
$P_{s,z}(t)$ —population (numbers) by size and zone at time t

the following being input parameters:

$P_{0,z}(t)$ —recruitment rate by zone at time t
G_s —proportion growing out of size s per unit time
G_0 —always = 1 (so that $P_{0,z}(t)$ is recruitment rate)
$\mu_{z_1\to z_2}$ —coefficient of migration from zone z_1 to zone z_2
M —natural mortality
$q_{s,g}$ —catchability by size and gear
$f_{z,g}(t)$ —effort by zone and gear at time t.

INPUT PARAMETER VALUES

Full details of how input parameters were estimated are given by Kleiber and Baker (fn. 2). The following is a summary.

The most complete catch and effort data sets that were available to us and that cover the three

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[2] Kleiber, P., and B. Baker. 1987. The North Pacific albacore simulation model. U.S. Natl. Mar. Fish. Serv., Southwest Fish. Cent., Admin. Rep. LJ-87-2, 38 p.

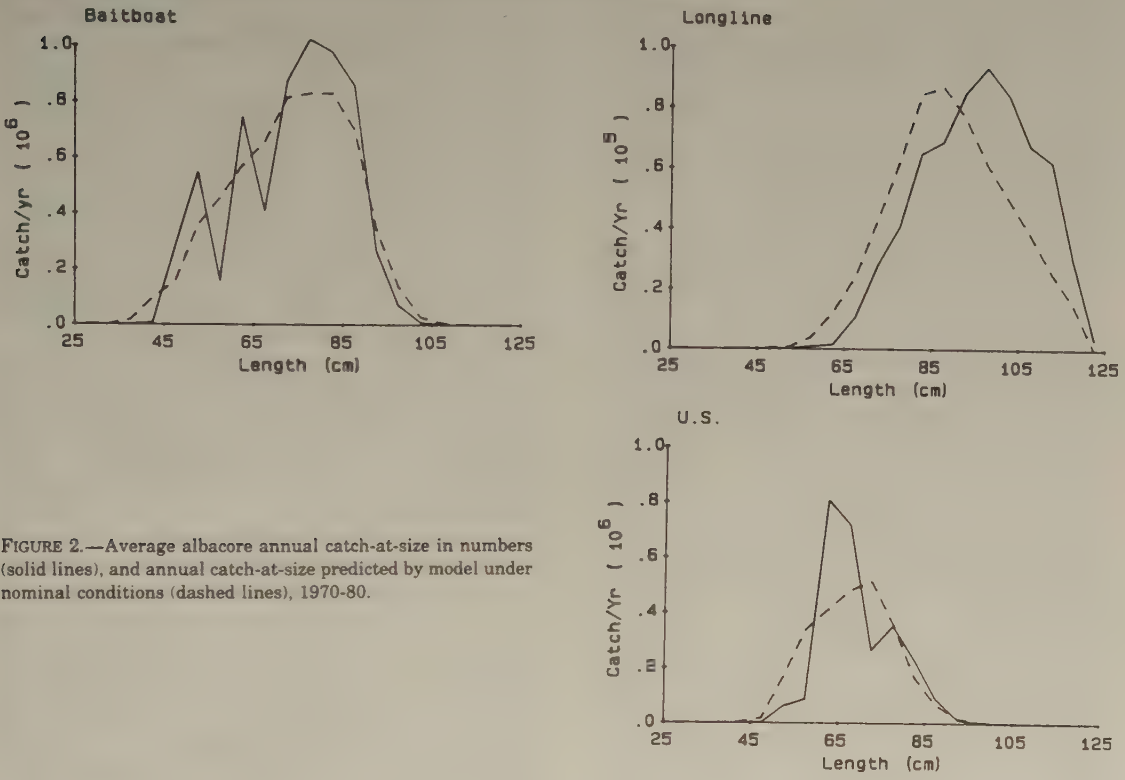
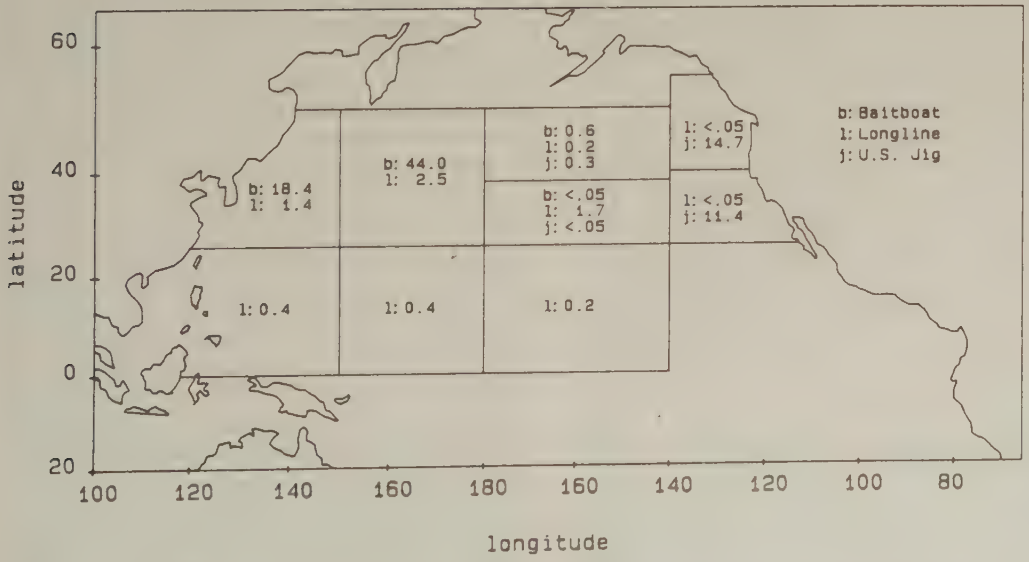


FIGURE 2.—Average albacore annual catch-at-size in numbers (solid lines), and annual catch-at-size predicted by model under nominal conditions (dashed lines), 1970-80.


60
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longitude
b: 18.4
l: 1.4
b: 44.0
l: 2.5
b: 0.6
l: 0.2
j: 0.3
l: <.05
j: 14.7
b: <.05
l: 1.7
j: <.05
l: <.05
j: 11.4
l: 0.4
l: 0.4
l: 0.2
b: Baitboat
l: Longline
j: U.S. Jig

FIGURE 3.—Model zones with average annual albacore catch (numbers × 10^5) by gear type, 1970-80.

major fleets span the years 1970 through 1980. We processed the data into an "average year", that is, the average (over the years 1970-80) of catch by size, zone, month, and gear and the average of effort by zone, month, and gear (Kleiber and Baker[3]). The effort values were used directly in the model and the catch and effort used to estimate other input parameters.

We estimated the 1970-80 average recruitment and preliminary catchability values by size and gear by use of a size-structured cohort analysis (Jones 1981). The catch-at-size vector necessary for this cohort analysis was obtained from the average year by aggregating over zones, averaging over months, and smoothing over size classes.

To conduct the cohort analysis, we needed to specify an average final cohort size, which was unknown to us. We tried a series of values and chose results for which the overall exploitation rate (catch divided by recruitment estimate) was close to the overall exploitation rate estimated from tagging. Tagged albacore have been released in the U.S. fishery at an average size of approximately 65 cm, and approximately 6% of the tags have been recovered (Laurs[4]). Nonreporting losses are small for the major fisheries that recovered the tags (Laurs[5]). Assuming a value of 10% for nonreporting and Type I and II tag losses of 12% and 0.098 year^{-1} respectively (Laurs et al. 1976), the exploitation rate of recruits to 65 cm should be approximately twice the raw recovery percentage. But the exploitation rate in the cohort analysis and the simulation model is based on recruits to 25 cm which should be approximately twice as numerous as recruits to 65 cm (based on growth and natural mortality rates used in the model). Therefore, the exploitation rate of recruits to 25 cm should be approximately equal to the raw tag recovery percentage (6%). We chose a cohort analysis with an exploitation rate of 6.3% as the basis for the results presented below except where we discuss sensitivity to exploitation rate for which we repeated the analysis several times starting at this point with a series of cohort analyses at a series of higher exploitation rates.

The cohort analysis yielded a Pacific-wide recruitment estimate. We apportioned one third of this recruitment to each of the three southern zones, where albacore larvae are predominantly found (Nishikawa et al. 1984).

Size-specific overall fishing mortalities obtained from the cohort analysis were apportioned to gear type by the proportion of the total catch at each size that is taken by each gear type in the average year. We then converted the fishing mortalities into catchabilities by dividing by the overall average effort for each gear type.

Size-specific growth coefficients, G_s, were the growth rates in length (*dl/dt*) at the upper end of each size class divided by the length of the size classes (5 cm). We estimated the growth rates from the derivative form of the von Bertalanffy growth equation

$$\frac{dl}{dt} = k(l_\infty - 1)$$

where l_∞ is 135.6 cm and k is 0.014 month^{-1} (Clemens 1961). We used these same values in the size-structured cohort analysis, which required input of growth information.

A value for natural mortality was also needed both in the cohort analyses and in the model. We used a value of 0.017 month^{-1} (0.2 year^{-1}) (Suda 1966).

The tag data would be a good source of information to estimate migration coefficients except that the tag recovery effort is not uniformly distributed and analytical techniques to deal with that situation are not well developed. To get a reasonable set of migration coefficients, we quantified the experience of three experts, scientists knowledgeable about the North Pacific albacore fisheries and the available tag data. We first asked the experts to identify the significant paths (movement from one zone to an adjacent zone) for each of a series of broad (10 cm) size classes. For each path we then asked how the intensity of migration via that path is distributed over the months of the year and we evaluated the average intensity by asking the experts the following question: On average, during the season of this migration, if 100 fish of the given size class are now in the origin zone, how many of these (irrespective of mortality) would be expected to be in the destination zone one month from now? We calculated the average migration coefficient for the particular path by

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[3] Kleiber, P., and B. Baker. 1986. Development of catch and effort data base for the North Pacific albacore simulation model. U.S. Natl. Mar. Fish. Serv., Southwest Fish. Cent., Admin. Rep. LJ-86-26, 21 p.

[4] Laurs, R. M. 1979. Results from North Pacific albacore tagging studies. U.S. Natl. Mar. Fish. Serv., Southwest Fish. Cent., Admin. Rep. LJ-79-17, 10 p.

[5] R. M. Laurs, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. March 1987.

$$\bar{\mu} = \ln\left[\frac{100}{100 - X}\right]$$

where X is the answer to the above question. The monthly migration coefficients were then obtained by scaling the distribution of intensity over months so that the average was equal to $\bar{\mu}$. The migration coefficients for the 10 cm size classes were then assigned to the smaller (5 cm) size classes used in the model, and the coefficients smoothed over size to soften discontinuities.

The pattern of movement represented by the migration coefficients can be summarized as follows: For immature fish (<85 cm) in the zones north of 25° north the pattern is vigorous seasonal movement toward the east in the summer and toward the west at other times. New recruits, which appear in the southern zones, migrate mainly northward throughout the year and are entrained in the east-west excursions of the northern zones. Mature fish (>85 cm) accumulate in the southern zones with brief movements northward in April and May.

RESULTS

When we ran the model with input values estimated as described above and with the effort of all fleets set at nominal levels, that is, the average seasonal and geographic pattern and magnitude of effort for the 1970s with the pattern repeated year after year, we found that after 10 years of simulation the seasonal and geographic pattern and magnitude of catch closely repeated itself year after year. Therefore in making comparisons of model results under different conditions, we allowed the model to run at least 10 years under a given repetitive annual regime before recording the catch results during 1 year of simulation.

In using the preliminary catchability values in the model, we found that the predicted catches were too low and the exploitation rate achieved (2.6%) was less than half the exploitation rate in the cohort analysis, which estimated those catchability values (6.3%). This is because the cohort analysis could not deal with geographic and seasonal variability. The fleets were presumed to be harvesting the ocean-wide population rather than the fish in a localized area and time as in the simulation model. We therefore scaled the catchabilities of each fleet upward to make the annual catches in number in the model (after 10 years of simulation) close to the real average annual catches (Kleiber and Baker fn. 2). With the corrected catchabilities, an exploitation rate of 5.1% was achieved and we took the results in this case to be our nominal (control) results (Fig. 2, Table 1).

We then made runs in which the original seasonal and geographic pattern of effort was maintained but the magnitude of effort of one of the fleets was either doubled or halved. We could then compare the annual catch of each fleet under the changed (experimental) conditions with the annual catch under nominal conditions.

TABLE 1.—Average albacore annual (1970-80) catch in numbers and metric kilotons (kt) by baitboat, longline, and U.S. fleets plus annual catch from model after at least 10 years of simulation under nominal conditions and under various conditions of altered fishing effort.

		baitboat		longline		U.S.	
		number (10⁶)	kt	number (10⁶)	kt	number (10⁶)	kt
average catch		6.29	57.52	0.68	13.30	2.65	19.56
nominal effort		6.87	55.12	0.66	9.47	2.67	18.32
baitboat effort	× 2	12.89	102.00	0.62	8.76	2.63	18.05
	÷ 2	3.55	28.69	0.69	9.86	2.69	18.46
longline effort	× 2	6.85	54.91	1.32	18.79	2.67	18.30
	÷ 2	6.88	55.23	0.33	4.75	2.67	18.33
U.S. effort	× 2	6.80	54.43	0.65	9.23	5.19	35.41
	÷ 2	6.90	55.49	0.67	9.59	1.35	9.32

The catch-at-size for the three fleets under nominal and experimental conditions is plotted in Figures 4 to 6. Changes in effort in one fleet appear to have little effect on the size distribution in the catch of any of the fleets.

The effect on amount caught is another matter. Total catch of all sizes, both in numbers and in weight, is given in Table 1. We obtained catch in weight by converting the number caught in each length category to weight using the length-weight relationship of Clemens (1961) and then by summing over length categories. The effects are summarized in Tables 2 and 3 where the change from nominal catch for each fleet is given for each experimental treatment. By far the largest effect of a change in effort of any fleet is the effect on its own catch. A doubling of the baitboat effort causes the largest between-fleet effect, which is a 7.5% depression of the longline catch in weight, a loss of approximately 700 t (Table 3). A similar loss to the baitboat fleet, due to doubling of U.S. effort, is only a 1.3% decrease in the baitboat catch (Table 3).

We tested the sensitivity of our results to the

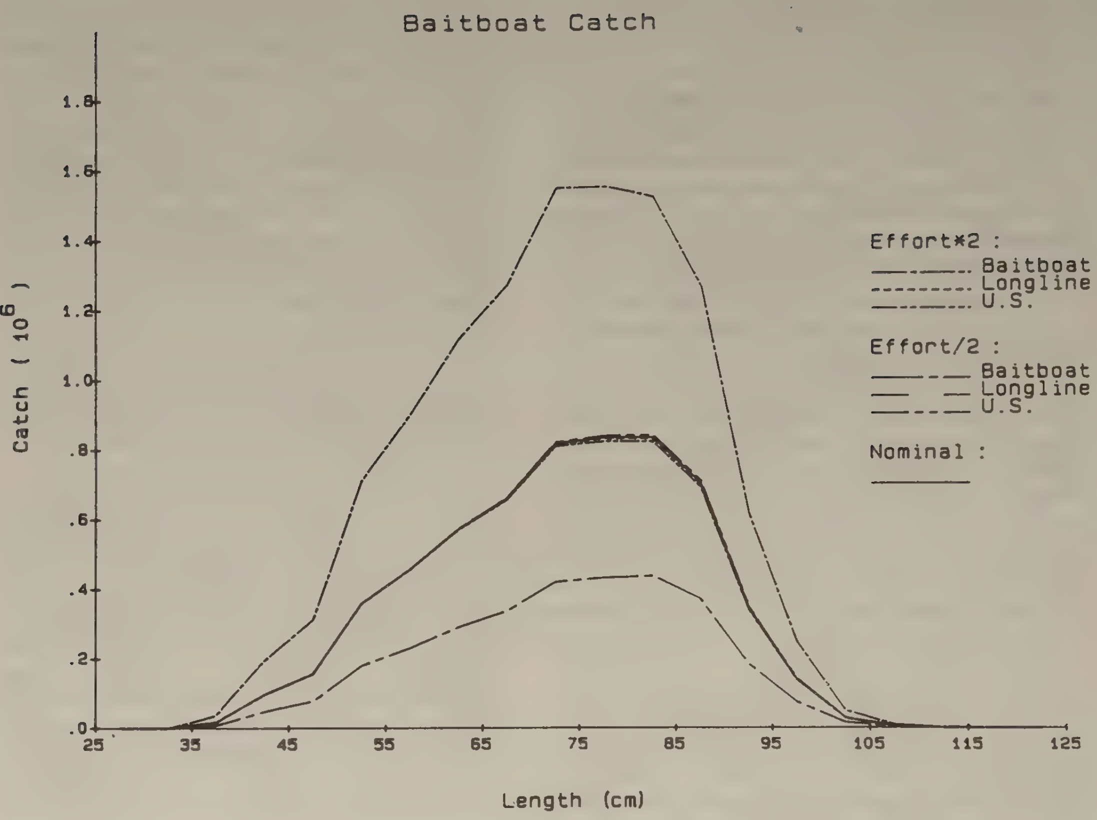

FIGURE 4.—Annual albacore baitboat catch-at-size in numbers predicted by the model under nominal and experimental conditions.

TABLE 2.—Interaction matrix for annual albacore catch in numbers. The values given are the differences between the catch under altered effort and the nominal catch (percent of nominal catch in parentheses).

cause ⇓ / effect ⇒		Δ catch: number × 10^6 (%)		
		baitboat	longline	U.S.
baitboat effort	× 2	6.02 (87.6)	−0.04 (6.1)	−0.04 (1.5)
	÷ 2	−3.32 (48.3)	0.03 (4.5)	0.02 (0.7)
longline effort	× 2	−0.02 (0.3)	0.66 (100.0)	0.00 (0.0)
	÷ 2	0.01 (0.1)	−0.33 (50.0)	0.00 (0.0)
U.S. effort	× 2	−0.07 (1.0)	−0.01 (1.5)	2.52 (94.4)
	÷ 2	0.03 (0.4)	0.01 (1.5)	−1.32 (49.4)

TABLE 3.—Interaction matrix for annual albacore catch in weight. The values given are the differences between the catch under altered effort and the nominal catch (percent of nominal catch in parentheses).

cause ⇓ / effect ⇒		Δ catch: kt (%)		
		baitboat	longline	U.S.
baitboat effort	× 2	46.88 (85.1)	−0.71 (7.5)	−0.27 (1.5)
	÷ 2	−26.43 (47.9)	0.39 (4.1)	0.14 (0.8)
longline effort	× 2	−0.21 (0.4)	9.32 (98.4)	−0.02 (0.1)
	÷ 2	0.11 (0.2)	−4.72 (49.8)	0.01 (0.1)
U.S. effort	× 2	−0.69 (1.3)	−0.24 (2.5)	17.09 (93.3)
	÷ 2	0.37 (0.7)	0.12 (1.3)	−9.00 (49.1)

overall exploitation rate by repeating the whole analysis at higher exploitation rates, starting with the cohort analysis, correcting catchabilities to give a new set of nominal results, and finally measuring the most sensitive interaction, the effect of doubled baitboat effort on the longline catch (Fig. 7). The degree of interaction is not affected very much when the exploitation rate is below 10%, but it rises quickly at higher exploitation rates.

DISCUSSION

Our results support the notion that fishery interaction is not of great consequence, at least for the North Pacific albacore fisheries typical of the

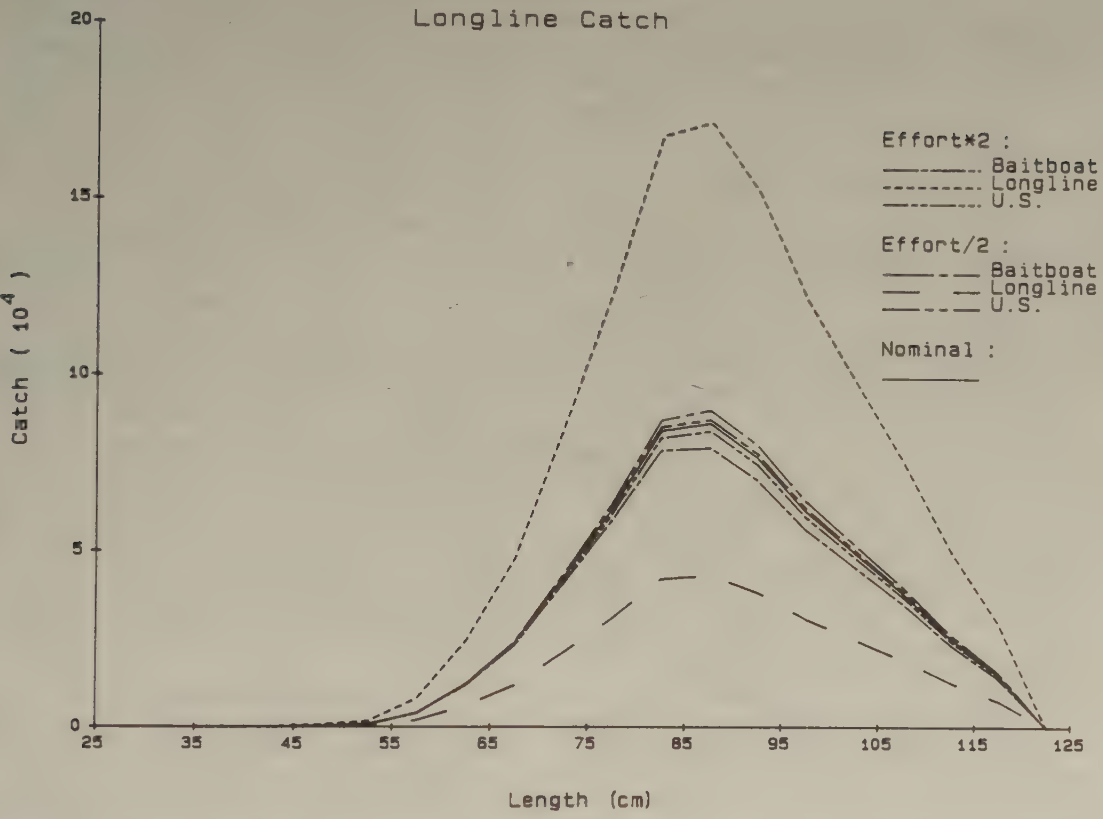

FIGURE 5.—Annual albacore longline catch-at-size in numbers predicted by the model under nominal and experimental conditions.

1970s. The reliability of this conclusion, of course, depends on the reliability of our simulation model, but in evaluating the behavior of the model, we should remember that what is important is the response of the model to experimental manipulation not the exactitude of the nominal behavior in comparison to real data. Of course, if the nominal behavior is outlandish, the responses to manipulation will be suspect. Therefore we used the average year as a signpost to tune the nominal results of the model into the range of plausible behavior, but we did not insist on exact duplication of the average year (itself an abstraction that never happened in reality).

A case in point is the longline catch, which under nominal conditions in the model is less (in weight) than any of the real annual longline catches for the years 1970-80. The average over those years is 13.3 metric kilotons (kt) per year whereas the nominal longline catch in the model is 9.47 kt/year (Table 1). The discrepancy is explained by the fact that the average size of fish in the model longline catch is less than the average size in the real longline catch, because large fish in the model migrate out of reach of the longline fleet more than they should. We have not corrected this problem because we are waiting for further information from tagging studies to get better estimates of migration coefficients. We expect the corrections to be quantitative refinements of the existing values and not a qualitative change in the current migration pattern in the model.

What is important in the current context is that bias in the nominal results is bound to show up in the experimental results as well. The migration coefficients were the same in both control and experimental situations in the model. Therefore, refinements to the coefficients are not likely to make much difference in the relative values in Tables 2 and 3, particularly in the percentages. It is pertinent that our conclusion of low interaction

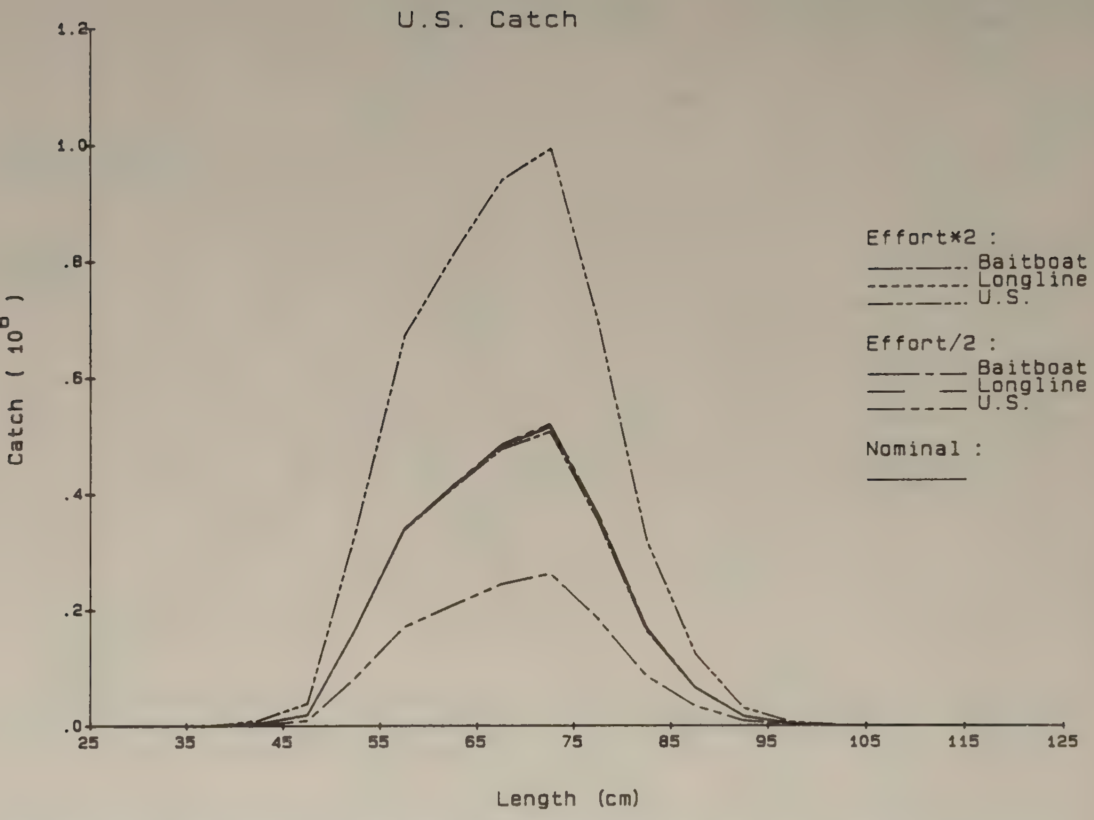

FIGURE 6.—Annual albacore U.S. catch-at-size in numbers predicted by the model under nominal and experimental conditions.

(expressed as percent) persisted through a series of updates of the model (such as changes in configuration of geographic strata) and inevitable updates and corrections of the fishery data base.

Though the nominal behavior of the model need not conform precisely to the mean behavior of albacore fisheries in the 1970s (however that might be defined), the behavior should, nonetheless, be a plausible representation of the albacore fisheries in that period. We have seen, for example, that our conclusion would be suspect if the actual exploitation rate were considerably higher than the 6% value that we assumed (Fig. 7), but such high exploitation levels would be contrary to the tag return results.

We have only tested the effects of changes in the magnitude of effort, not changes in seasonal and geographic pattern of effort, which might cause the fleets to overlap much more than they do. However, our experimental treatment of doubling the effort of a fleet is tantamount to adding

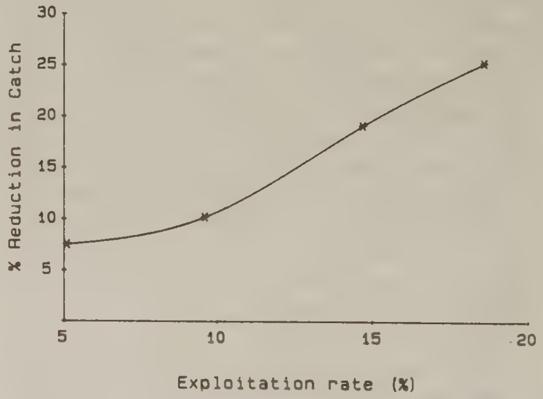

FIGURE 7.—Sensitivity of interaction to overall exploitation rate. The ordinate is the percent reduction from nominal levels in annual albacore longline catch in weight as a result of doubling the baitboat effort.

a completely overlapping, competing fleet. The response of each fleet to doubling of its own effort was close to a 100% increase in catch (Tables 2, 3), indicating that the degree of competition was low. Therefore, it would be difficult to design a realistic experimental treatment that 1) would be simply a shift in the geographic and seasonal pattern of effort in one fleet (not a change in magnitude), and 2) would have a strong impact on another fleet.

A legitimate question is whether our conclusions, which are based on 1970s data, can be extrapolated to the current conditions. The most striking change in recent years is the emergence of the gill net fishery for albacore, which now takes approximately 20% of the total catch. However, because the total catch has not increased, the exploitation rate must still be mild, and we would expect that interaction between fleets would also still be mild. We cannot use our model to estimate interaction quantitatively in this situation because we lack detailed data on the gill net fishery.

CONCLUSIONS

The implication of our results is that fleet interaction is not likely to be significant if the pattern and magnitude of effort in the 1970s are maintained. This assessment could change if the overall exploitation rate increases considerably. The recent emergence of the gill net fishery could be of significance in this regard. The levels of annual catch that have been reported by this fishery are not likely to be of concern, but the significance cannot be confidently evaluated unless detailed catch, effort, and size distribution data are made available.

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Pericardial and vascular pressures and blood flow in the albacore tuna, *Thunnus alalunga*

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Summary. Pericardial, ventricular, and dorsal aortic pressures, and blood flow were measured in tabled, anesthetized albacore tuna, *Thunnus alalunga* (7.8–10.7 kg) captured at sea off Monterey, California (USA) during August 1985. Mean pericardial pressure was $-10.0/-2.6$ cm H_2O (Systolic/Diastolic, [S/D]) and mean pericardial pulse pressure was 7.5. Heart rate averaged 87 beats per minute. Mean ventricular pressure was 97.0/12.9 cm H_2O [S/D] and mean dorsal aortic pressure was 64. High ventricular and dorsal aortic pressures of albacore reflect the perfusion requirement of its metabolically active tissues and compensate for the energy losses resulting from blood flow through the gills to arterial heat exchanger to capillaries and again back to the venous heat exchanger. As in elasmobranchs, the remarkably high pericardial pulse pressure, large pericardial volume, and negative pericardial pressure in the albacore suggest that its pericardium is more rigid than that of most teleosts and thus facilitates cardiac filling. Published cardiac output values for most non-tunas, when corrected for body size differences, are less than the mean weight specific cardiac output of albacore (29.4 ml/kg per min, range 12.9–51.9).

Key words: *Thunnus alalunga* – Tuna – Vascular pressures – Cardiac output

Introduction

Tunas (family Scombridae) are highly specialized pelagic fishes renowned for their continuous swimming and transoceanic migrations. They possess numerous adaptations that enable them to sustain high cruising speeds for extended periods (Beamish 1978). Included among these are a streamlined body shape and a high aspect ratio lunate tail which reduce drag and increase swimming efficiency (Magnuson 1978). Tunas also maintain an elevated body temperature which positively affects the metabolic efficiency of their red and white swimming musculature (Stevens and Neill 1978). Metabolic heat generated by their swimming muscles is conserved in the vascular counter-current heat exchangers *(retia mirabilia).* Vascular supply to these exchangers is via cutaneous arteries and veins that are best developed in the family Scombridae (Graham 1975; Graham and Diener 1978).

The high metabolic activity of a swimming tuna requires the support of a circulatory system capable of delivering high volumes of blood and large quantities of oxygen. Correspondingly, tunas relative to other fishes have greater blood hemoglobin concentrations (Klawe et al. 1963), a larger blood volume (Laurs et al. 1978), and larger gill surface area (Muir and Hughes 1969). A tuna's heart, unlike other teleosts, must additionally pump blood at sufficient pressures to compensate for the energy losses incurred circulating blood from the gills to the heat exchanger to capillaries and then again back through the exchanger (Graham 1975; Graham and Diener 1978). Tunas have large hearts (Graham et al. 1983) and ultrastructural and histochemical analyses (Tota 1978, 1983; Breisch et al. 1983) suggest that this organ can sustain high levels of physiological performance. Moreover, the vascular pressure and heart rate reported for the albacore tuna by Breisch et al. (1983) exceed those of most other fishes.

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Tunas are exceedingly difficult to capture and maintain in captivity, which precludes their use in most experimental studies. By working at sea with freshly captured albacore we were able to partially surmount these limitations. The objectives of our study were to measure the pericardial and vascular pressures and the cardiac output of freshly captured, anesthetized, restrained, and ventilated albacore *(Thunnus alalunga* Bonnaterre).

Materials and methods

All studies were conducted off Monterey, California (USA) aboard the NOAA RV *David Starr Jordan* in August 1985. Thirty-three albacore were captured using feathered jigs trolled just beneath the surface at 5 knots. Immediately following a jig strike the ship was slowed and the fish was brought along side by a hydraulic hoist and lifted to the deck by hand, usually within 1 min. The hook was immediately removed from its mouth and its gills irrigated with running seawater. It was then immobilized with either unbuffered gallamine triethiodide (3–4 mg injected into the lateral cutaneous vessel) or by postcranial spinalectomy. The fish was rushed to the laboratory where it was placed supine on a V-board and ventilated with oxygenated seawater (15.8°–17.0 °C, $\bar{x} = 16.5$ °C, 1.98 l/min) containing 0.1 g/l of tricaine methane sulphonate (MS222). Depending upon each specimen's reponse level anesthetic was intermittently added to ventilation water. Because of uncertainties about fish condition, experimental protocols were in most cases done in the following succession: pericardial pressure, ventricular pressure, blood flow, and dorsal aortic pressure.

Pericardial and ventricular pressures

An 18 ga needle was inserted percutaneously into the pericardial space and connected to a Statham P23Db pressure transducer by a catheter filled with teleost saline (Fig. 1). For zero reference on each transducer a second saline-filled catheter was positioned outside the animal's body and at the same level as the pericardial catheter tip. The entire procedure took about 5 min. Pressure recordings were amplified (Honeywell Electronics for Medicine, V2203A) and recorded with a Gould oscillograph (Brush 260). Needle catheters were routinely flushed from a saline-filled syringe reservoir common to the gauge and the catheter (Fig. 1).

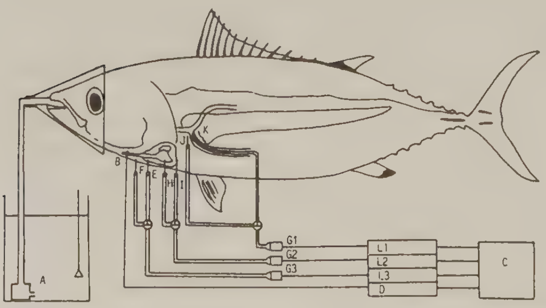

Fig. 1. Recording arrangement for *Thunnus alalunga*. *A* oxygenated reservior; *B* flow probe; *C* Gould oscillograph; *D* flow meter and DC amplifier; *E* pericardial catheter; *F* zero reference for pericardium; *G, 1, 2, 3* Statham pressure transducers; *H* ventricular catheter; *I* zero reference for ventricle; *J* zero catheter for dorsal aorta; *K* dorsal aorta catheter; *L, 1, 2, 3* pressure amplifiers

Ventricular catheterization was also done percutaneously from the ventral body surface by advancing an 18 ga transducer-connected thin-walled needle filled with heparinized teleost saline into the ventricular lumen (Fig. 1). The position was verified by pressure signal and a zero reference catheter was mounted at the level of the ventricular needle. About 5 min was required for this procedure.

Dorsal aortic pressure

Access to the dorsal aorta was via a cutaneous artery. An incision was made on the mid lateral side of the fish about 2 cm ventral and 5 cm caudal to the pectoral fin (Fig. 1). Removal of the subcutaneous connective tissues revealed the lateral cutaneous vessels and associated fascia. The lateral cutaneous artery was identified and cannulated with PE 90 tubing. To control blood flow during this procedure a silk ligature was passed around the vessel on proximal and distal sides of the cannulation site. The catheter, marked in cm gradations, was advanced 7 to 9 cm anteriorly, depending on the incision site and the size of the fish, to the junction of the cutaneous artery and dorsal aorta, and was secured with a ligature. Pressure measurements and a zero reference were as described above. This procedure required about 20 min.

Ventral aortic flow

An electromagnetic flow probe (Carolina Medical Electronics) was placed on the ventral aorta (Fig. 1). A median incision was made along the gill isthmus and the urohyal bone separated. The ventral aorta was exposed by removing all tissues including those attached to the vessel. A flow probe with a diameter similar to the vessel was attached by gently lifting the vessel away from underlying structures. Once the probe was in place, the incision was closed and held securely by two towel clamps. The flow probe implantation required about 30 min.

At the end of the experiment the fish was sacrificed for in vitro calibration of the flow probe. The portion of the ventral aorta where the probe had been placed was excised and one end was affixed to a three-way stopcock connected to a vertically positioned syringe. The free end of this vessel was opened into a dish of teleost saline. The probe used in the experiment was then mounted on the vessel and known volumes of teleost saline were manually injected through the vessel in a pattern that mimicked the flow records. A Talos X-Y digitizer interfaced to a Tektronix intelligent terminal was used to analyze flow data.

Results

Successful studies were carried out on 19 of the 33 fish tested (Table 1). No differences were found between fish that were immobilized with gallamine triethiodide (n = 13) and those that were spinalectomized (n = 6). Heart rate ranged from 50 to 120 beats per minute (bpm, $\bar{x} = 87$). Ventricular systolic pressure [S] ranged from 55.0 to 150.0 cm H_2O ($\bar{x} = 97.0$) and diastolic pressure [D] from −5.0–63.0 cm H_2O ($\bar{x} = 12.9$).

Table 1. Heart rate (n = 19), ventricular (n = 17), and pericardial pressures (n = 15) of *Thunnus alalunga*

Albacore No.	Fork length (mm)	Body weight[a] (kg)	Heart rate (bpm)	Ventricular pressure			Pericardial pressure		
				Systole	Diastole (cm H_2O)	Pulse	Systole	Diastole (cm H_2O)	Pulse
2	777	9.2	102	120.0	50.0	70.0	−15.0	−14.0	1.0
3	775	9.1	102	85.0	−5.0	90.0	−9.5	−9.0	0.5
4	800	9.9	108	56.0	30.0	26.0	−6.9	−5.8	1.1
5	780	9.3	100	120.0	10.0	110.0	−5.0	−4.0	1.0
7	750	8.3	60	85.0	−5.0	90.0	−6.0	−5.0	1.0
9	760	8.6	75	74.0	63.0	11.0	−18.0	−8.9	9.1
12	750	8.3	50	95.0	5.0	90.0	−19.8	6.6	26.4
13	780	9.3	120	125.0	0	125.0	−20.0	0	20.0
16	820	10.7	100	140.0	50.0	90.0	0	3.3	3.3
17	790	9.6	120	–	–	–	−6.6	−3.3	3.3
22	810	10.3	106	57.0	0	57.0	–	–	–
23	795	9.8	83	131.0	5.7	125.3	−8.3	13.2	21.5
25	760	8.6	107	103.0	5.7	97.3	−9.9	0	9.9
26	770	9.0	79	150.0	10.0	140.0	−16.5	−9.9	6.6
27	740	7.9	50	–	–	–	–	–	–
28	800	9.9	107	120.0	0	120.0	–	–	–
31	770	9.0	51	55.0	0	55.0	−4.0	−1.0	3.0
32	760	8.6	71	60.0	0	60.0	−5.2	−0.7	4.5
33	735	7.8	59	73.0	0	73.0	–	–	–
Mean	–	–	87	97.0	12.9	84.1	−10.0	−2.6	7.5
Standard error	–	–	±6	±7.7	±5.2	±8.6	±1.6	±1.8	±2.2

[a] Estimated by regression, $M = 4.514 \times 10^{-5} L^{2.8746}$ (Dotson 1976), where M is mass in grams and L is fork length in mm

Table 2. Simultaneous ventricular and dorsal aortic pressures of *Thunnus alalunga* (n = 5) showing the transbranchial pressure drop. See Table 1 for body size data

Albacore No.	Ventricular pressure (cm H_2O)	Dorsal aortic pressure (cm H_2O)	Transbranchial pressure drop (cm H_2O)	Percent drop
13	125	90	35	28
25	103	73	30	29
26	150	30	120	80
28	120	96	24	20
32	60	30	30	50
Mean	112	64	48	41
Standard error	±15	±14	±18	±11

Table 3. Cardiac output (n = 5) of *Thunnus alalunga*. See Table 1 for body size

Albacore No.	Heart rate (bpm)	Stroke volume (ml/stroke)	Cardiac output (ml/min)	Weight-specific cardiac output (ml/kg per min)
25	107	2.5	267.5	31.1
27	107	1.7	181.9	23.0
28	107	4.8	513.6	51.9
32	71	3.4	241.4	28.1
33	59	1.7	100.3	12.9
Mean	90	2.8	260.9	29.4
Standard error	±10	±0.6	±69.4	±6.4

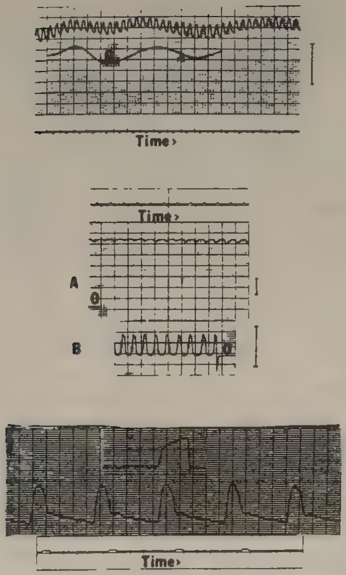

Fig. 2. *Top* Recording of ventricular pressures in *Thunnus alalunga* showing the effect of ship roll. Lower trace is the zero reference. Vertical scale = 200 cm H_2O. Time marks are 1 s. *Middle* Recordings of dorsal aorta (A) and ventricular (B) pressures in *Thunnus alalunga*. Zeroes are marked on the tracings. Vertical scales: A = 20 cm H_2O, B = 200 cm H_2O. Time marks are 1 s. *Bottom* Ventral aorta blood flow in *Thunnus alalunga*. Upper trace is a record for 3 ml saline passed through the same probe. Time marks are 1 s

Pericardial systolic pressure was successfully measured in 15 albacore and in all cases was either negative or zero (Table 1). Mean pericardial pressure during systole was −10.0 cm H_2O and during diastole was −2.6 cm H_2O. The mean pericardial pulse pressure (the difference between the mean D and S pressures) was 7.5 cm H_2O. Dorsal aortic pressure (Table 2, Fig. 2) ranged from 30 to 96 cm H_2O ($\bar{x} = 64$). In cases where both were measured in the same fish, ventricular pressure always exceeded that in the dorsal aorta.

A typical electromagnetic flow output is shown in Fig. 2. Stroke volume ranged from 1.7 to 4.8 ml and increased with body size (Table 3). Mean cardiac output was 260.9 ml/min. The weight-specific cardiac output also increased with fish size ($\bar{x} = 29.4$ ml/kg per min, range 12.9–51.9).

Discussion

There have been few studies reporting teleostean pericardial pressures. Freadman (1983) measured this in swimming bluefish *(Pomatomus saltatrix*, −6.4/−2.6 cm H_2O [S/D]) and tautogs (*Tautoga onitis*, −2.6/0.7 cm H_2O [S/D]. The pericardial pulse pressures of these fishes are much less than that of tabled albacore (Table 1).

How might large negative pressure affect albacore heart function? In elasmobranchs a negative pericardial pressure facilitates aspiration of blood for cardiac filling (Johansen 1965; Sudak 1965; Shabetai et al. 1985). Yet, the pericardial pulse pressures reported by Shabetai et al. (1985) for active pelagic species (blue shark 3.9 cm H_2O, bat ray 2.9, mako shark 1.9, and the great white shark 3.2) are much less than in albacore (7.5). Features of elasmobranch anatomy that relate to its cardiac filling mechanism are the semi-rigid pericardium and the large ratio of pericardial to cardiac volume, the mean ratio is 3.8 for all species studied by Shabetai et al. (1985). Teleosts are generally regarded as having a more compliant pericardium than elasmobranchs (Satchell 1970, 1971) but comparative biomechanical studies are lacking. Preliminary studies in our laboratory do reveal that pericardial compliancy of albacore is similar to that measured for the transverse septum of elasmobranchs. Also, measurements (using self-leveling silastic rubber) in two 9 kg albacore yielded pericardial volumes of about 50 ml and thus a ratio of pericardial to cardiac volume of 2. Thus, our preliminary compliancy and volume studies together with the measured high pulse pressures lead us to speculate that the albacore may have a more rigid pericardium than other teleosts and that this, as in elasmobranchs, facilitates cardiac filling.

Tunas, swordfish, and elasmobranchs exhibit a high level of cardiac organization (Tota 1978, 1983; Briesch et al. 1983; Emery 1985). The well developed compact myocardium of tuna heart resembles the homeotherm ventricle in having high capillary density (Tota 1983) and is capable of generating high pressure. The mean systolic ventricular pressure (97.0 cm H_2O, Table 1) of albacore is higher than reported for all other fishes (Johansen 1962; Johansen et al. 1966; Stevens et al. 1972; Shabetai et al. 1985). The heart rate, pericardial, ventricular, and dorsal aortic pressures reported here are variable, which could be attributed to factors such as the effects of capture, handling, MS222, and the length of time required to conduct the experiments. Variability of the dorsal aortic pressure is further attributable to a decline in viability of specimens late in the experimental protocol (e.g., fish 26 and 32, Table 2). High dorsal aortic pressures (maximum 96 cm H_2O), however, were recorded in several instances. These are similar to values reported by

Briesch et al. (1983, 107 cm H_2O) and are also higher than values reported for most fishes, (e.g., *Onchorhynchus tschawytscha* 64 cm H_2O, Robertson et al. 1966; *Onchorhynchus nerka* 56, Smith et al. 1967; *Salmo gairdneri* 35, Stevens and Randall 1967; *Squalus acanthias* 39, Burger and Bradley 1951).

Although the increase in surface area of the *rete* reduces vascular resistance, the albacore still needs to conserve a high vascular pressure to compensate for the energy loss imposed by the gills and heat exchanger and ensure perfusion of its metabolically active tissues. Data for fish 13, 25, and 28 (Table 2) show that blood flow across the gills resulted in an average pressure drop of 30 cm H_2O (26%), which is low relative to that recorded for most fishes. From data summarized for seven species by Satchell (1971), we estimated pressure drops of from 22 to 79%. We do not know how factors such as anesthesia, oxygenated water, and the supine, emergent position of the albacore may have affected branchial resistance.

The mean transbranchial pressure drop we recorded for fish 13, 25, and 28 (30 cm H_2O) is, however, higher than the colloidal osmotic pressure values reported by Hargens (1971) for active temperate zone fishes (range 18–23 cm H_2O). Saltwater teleosts are hyposmotic and constantly face problems of water loss. Vascular pressure has been shown to increase transbranchial water loss in trout (Davie and Daxboek 1982). Our data suggest that the high vascular pressures in tunas would have the same effect. Thus, albacore may need to maintain higher colloidal osmotic pressures or have a specialized gill epithelia to mitigate water loss.

Estimates of cardiac output differ among species. They vary with activity state and temperature, and are also dependent upon the measurement techniques used (Metcalfe and Butler 1982). Size is also important (Schmidt-Nielsen 1984) and values for weight-specific cardiac output have been mostly obtained for fishes weighing less than 1 kg. Our cardiac output estimate for an 8.6 kg albacore (Table 3) is similar to that measured for this species by White et al. (in preparation, 33.8 ml/kg per min). However, for reasons given above, direct comparison of our data with other fish species is not easy. For example, the highest known cardiac output values are for restrained skipjack tuna (*Katsuwonus pelamis*, mean weight 1.6 kg, Stevens 1972). These were calculated by the Fick method and ranged from 50–80 ml/kg per min at 23–25 °C. In the case of resting non-tunas, values for rainbow trout (*Salmo gairdneri*, 0.2–0.4 kg, 15–30 ml/kg per min at 4–8 °C; Stevens and Randall 1967) and cod (*Gadus morhua*, 0.4–1.0 kg, 29.1 ml/kg per min at 10 °C; Pettersson and Nilsson 1980) are among the highest reported. Since weight-specific cardiac output declines with increased body size (Schmidt-Nielsen 1984) the above values decline when extrapolated to 8.6 kg. The metabolic rates of fishes are generally an order of magnitude lower than mammals yet the relationship between metabolic rate and body size in these two groups remains the same (Schmidt-Nielsen 1975) and it can be reasonably assumed that cardiac output and oxygen consumption are correlated (Schmidt-Nielsen 1984). Stahl (1967) worked out the mammalian relationship between cardiac output ($\dot{Q}_h$, in ml/min) and body weight (M_b, in kg) as

$$\dot{Q}_h = 187 M_b^{0.81}$$

Assuming that fish follow a similar relationship we calculated that the weight-specific cardiac output values for rainbow trout and cod would be 10 and 18 ml/kg per min respectively at 8.6 kg. That for a skipjack would be 43 ml/kg per min. Thus at comparable body sizes cardiac outputs of the two non-tunas are less whereas the cardiac output of the skipjack remains higher than albacore. The high cardiac output of skipjack may reflect errors inherent in the Fick calculation (Stevens 1972; Metcalfe and Butler 1982). It may also relate to the skipjack's higher metabolic rate (discussed in Graham and Laurs 1982). When the above equation is used to compare cardiac outputs of elasmobranchs at 8.6 kg (all weighing between 0.5 and 7 kg, Murdaugh et al. 1965; Metcalfe and Butler 1982), the values are lower than the albacore.

High heart rate, pericardial pulse pressure, and ventricular pressure are all indicative of high cardiac performance in the albacore. We are uncertain about the extent that restraint and anesthesia affect cardiac function. Thus, further work on free swimming albacore is needed to define the scope of its cardiac function.

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Use of Fish Eggs and Larvae in Probing Some Major Problems in Fisheries and Aquaculture

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Abstract.—Studies of the early life history of marine fishes have progressed greatly in the quarter century since the pioneering work of Sette, Ahlstrom, and others. A brief history of this recent era points out the many ways in which eggs and larvae have been used to address central problems of fishery dynamics, management, and culture. Challenges and opportunities await early life historians in the areas of fish distribution, biomass estimation, species identification, recruitment, species interactions, aquaculture, enhancement, pollution assessment, definition of subpopulations, and production. Early life history studies have acquired considerable relevance to society as well as to science.

I was pleased and flattered to be asked to be the keynote speaker to this meeting of the Early Life History section of the American Fisheries Society. The papers of this meeting are very impressive and comprehensive, much more so than those of the very first Larval Fish Conference in the United States, which was held at Lake Arrowhead, California, in October 1963. The proceedings of that early conference appeared in volume X of the California Cooperative Oceanic Fisheries Investigations Reports of 1965. Figure 1 is a photograph of the conference contributors.

In 1963, although we had some data which showed that fish eggs and larvae could be important tools in the study of fish populations, we still had much to prove. Now, many of the papers being given at this 1986 conference are proof of this early premise. This paper is a personal perspective on studies of early life history of fish. It is intended to give a historical view of some of the reasons fishery scientists find the subject interesting and to suggest what the future may hold for those of us who continue with it. Although I cannot possibly cover every aspect of the early life history of fishes, I hope to make the point that fisheries science has benefited a great deal from the subject.

The need for fisheries management is one good reason to bring us together and I would like to aim my remarks towards that end, recognizing, of course, that foremost we are biologists trying to answer the important basic question of how fish eggs and larvae survive in natural waters.

Sette, Ahlstrom, and Schaefer

In California, I was able to meet and associate with some of the pioneers in the study of fish eggs and larvae. These people are becoming fewer and those with an early vision of the importance of this field to fisheries science are no longer with us. I am referring to scientists like Elbert H. Ahlstrom, Milner B. Schaefer, and Oscar Elton Sette, each of whom would have made a better speaker than I. However, I did have substantial contact with each of them and I would like to start this talk with a few anecdotes which should give you an impression of how important they were to the study of the early life history of fishes in relation to fisheries.

Sette (Figure 2) was a fishery biologist for the U.S. Fish and Wildlife Service who believed that an understanding of fish eggs and larvae and what affected them in the sea would lead us to an ability to predict the size of incoming year classes. When the population of Pacific sardine *Sardinops sagax* (then known as *S. caerulea*) suffered from its now famous collapse in the 1940s, he was sent by the federal government to set up a U.S. initiative to find out what happened. Figure 3 is from his 1943 paper (Sette 1943b) on setting up a research program to determine how fishing affected the sardine resource. In it you can see all the elements for determining what factors affect an incoming year class to a fishery. In particular, the importance of fish eggs and larvae is clearly pointed out.

Ahlstrom (Figure 4) was Sette's collaborator, and it was he who was given the day-to-day responsibility to carry out systematic ichthyoplankton surveys. This was the origin of the now unique larval fish time series of California and Baja California species which began in 1939. Ahlstrom believed that at least two important questions could be answered with these surveys: How is the Pacific sardine distributed? and How is

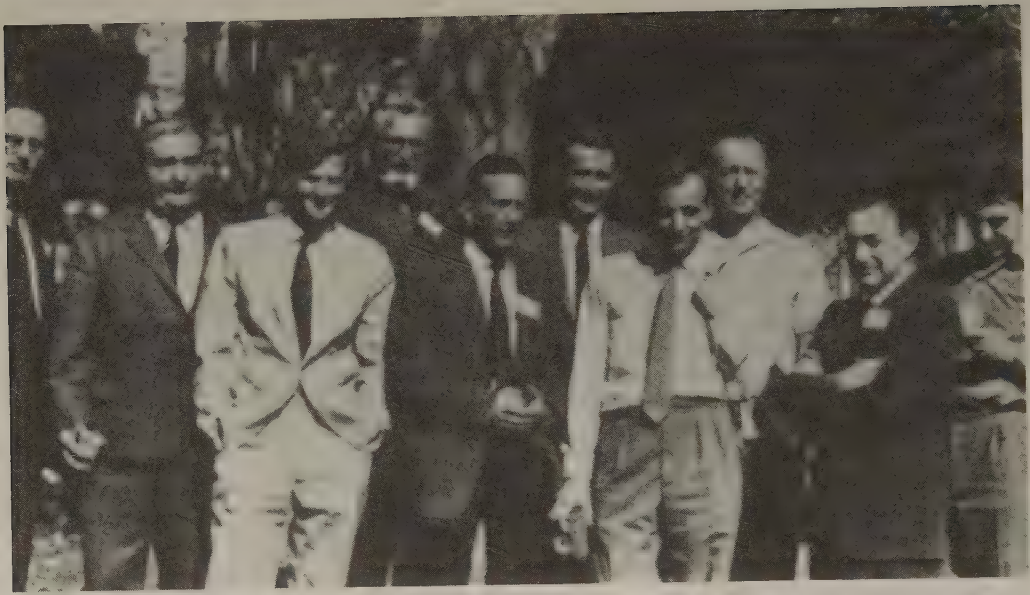

FIGURE 1.—Participants in the first conference on the early life history of fishes, Lake Arrowhead, California, October 1963. Left to right: George O. Schumann (La Jolla), Wilhelm Einsele (Austria), Fred Holliday (Aberdeen), John Isaacs (La Jolla), Horst Schwassman (La Jolla), James E. Shelbourne (Lowestoft), John Blaxter (Aberdeen), Elbert H. Ahlstrom (La Jolla), Reuben Lasker (La Jolla), Gotthilf Hempel (Hamburg).

the Pacific sardine population changing with time? To our everlasting benefit, Ahlstrom chose not only to look for Pacific sardine eggs but, because of his deep interest in systematics and ontogeny, set out to name and identify all of the eggs and larvae that were caught by the plankton nets deployed for Pacific sardine.

FIGURE 2.—Oscar Elton Sette, about 1949.

In a less complicated world where direct contact with Washington for assistance was possible, funds were always ample for these surveys. Joining with the Fish and Wildlife Service was the Scripps Institution of Oceanography, headed in the 1950s by Roger Revelle, who saw the enormous value in such surveys not only for monitoring fish populations but for describing the oceanography and ecology of the California Current system. The California State Legislature provided funds for the Marine Life Research Group at Scripps Institution of Oceanography at the request of a former director, Harald Sverdrup, and it continues today as a partner in what is known as the California Cooperative Oceanic Fisheries Investigations or CalCOFI. From the surveys we learned that the collection and identification of fish eggs and larvae can tell us where fish reside, when they spawn, and how they are related to each other numerically and ontogenetically.

Schaefer (Figure 5) was one of the original Pacific sardine investigation scientists with Sette

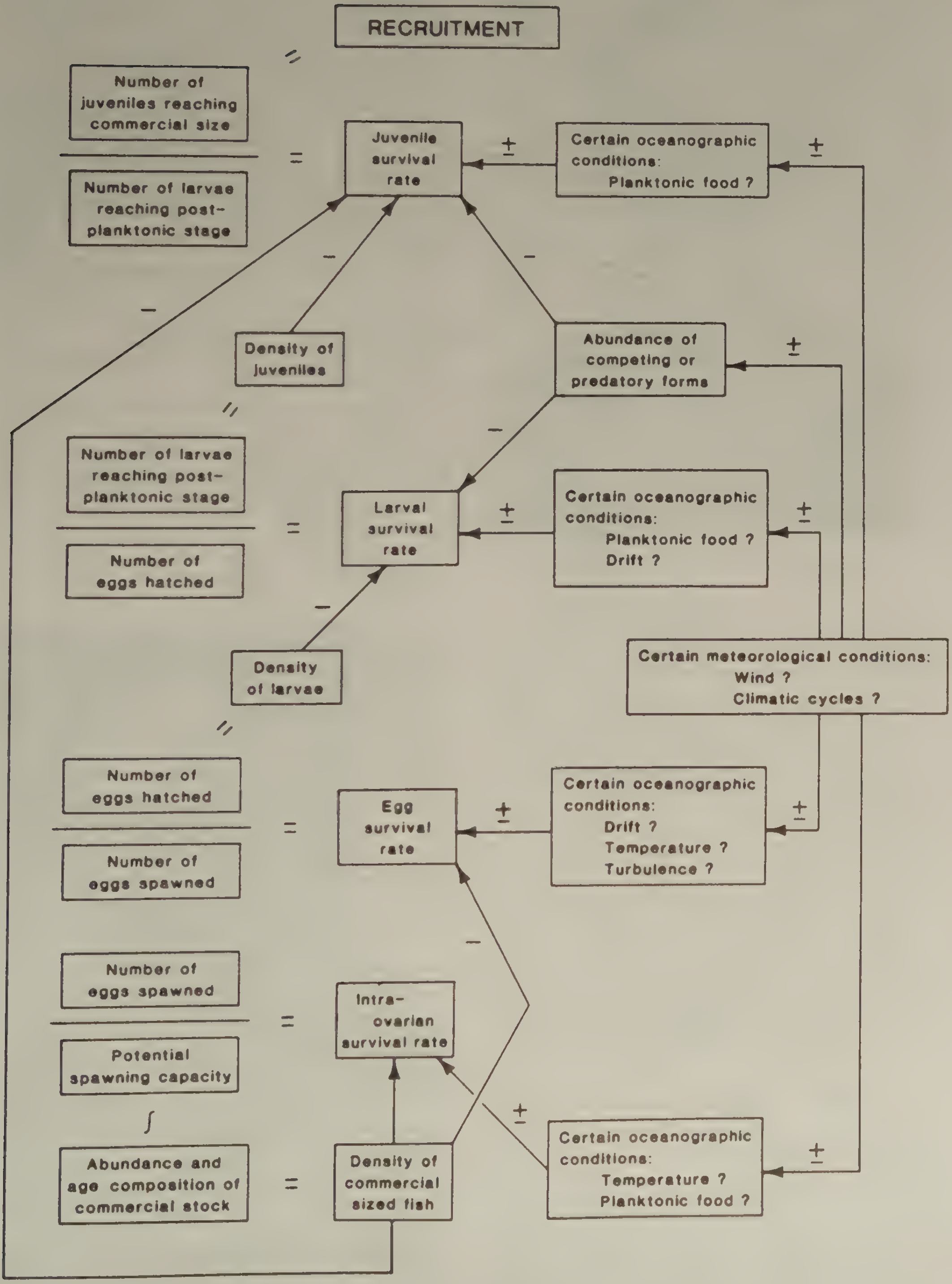
RECRUITMENT
Number of juveniles reaching commercial size
Number of larvae reaching post-planktonic stage
=
Juvenile survival rate
Certain oceanographic conditions: Planktonic food ?
±
±
–
–
–
Density of juveniles
Abundance of competing or predatory forms
±
–
Number of larvae reaching post-planktonic stage
Number of eggs hatched
=
Larval survival rate
±
Certain oceanographic conditions: Planktonic food ? Drift ?
±
–
Density of larvae
Certain meteorological conditions: Wind ? Climatic cycles ?
Number of eggs hatched
Number of eggs spawned
=
Egg survival rate
±
Certain oceanographic conditions: Drift ? Temperature ? Turbulence ?
±
–
Number of eggs spawned
Potential spawning capacity
=
Intra-ovarian survival rate
∫
Abundance and age composition of commercial stock
=
Density of commercial sized fish
±
Certain oceanographic conditions: Temperature ? Planktonic food ?
±

FIGURE 3.—Sette's plan to study recruitment of the Pacific sardine, 1943.

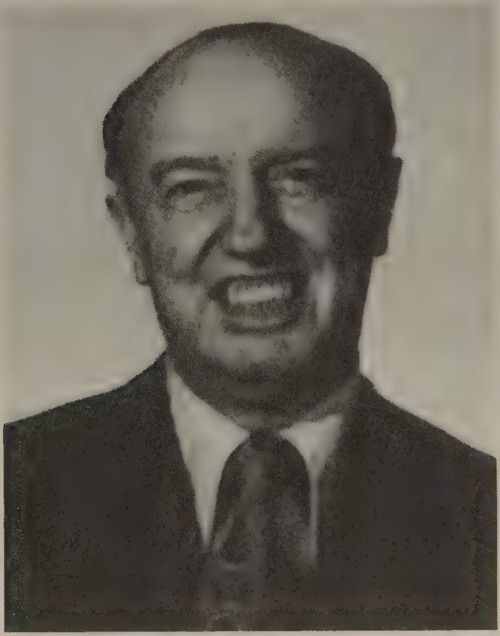

FIGURE 4.—Elbert H. Ahlstrom, about 1969.

in 1946 but, to my knowledge, he never worked on fish eggs or larvae. Why then, do I include him in this essay? The reason, quite simply, is that he had the major role in writing the section on fisheries for the National Academy of Sciences report on "Oceanography in the 1960s." The post-Sputnick era promised increased money for science and it was Schaefer who pointed out the potential importance of the study of fish eggs and larvae to aquatic science and fisheries in particular. We probably all owe a debt to him.

I make no claim that the following is an exhaustive survey of who has done what in this remarkable field. Rather, I have chosen to talk about the attempts made at solving some major problems in fisheries science by studying fish eggs and larvae. Examples are taken mostly from the west coast of the USA with which I am personally familiar.

Some Major Problems in Fisheries Science

The major scientific problems in fisheries science today, by my definition, are those which fishery scientists agree need to be solved to facilitate rational management of fisheries throughout the world. I have listed those which I believe are the most pressing; attempts to solve them have involved fish eggs and larvae. It is surely not an exhaustive list.

(1) *Distribution:* Where are the fish?

(2) *Biomass estimation:* How many fish are in the sea?

(3) *Species identification:* What fish are there?

(4) *Recruitment:* How many fish will be available to a fishery next year? This question subsumes others. Can the magnitude of recruitment be predicted? What are the biotic and abiotic factors affecting recruitment? To what extent can we fish a population without endangering successive year classes? How and why do populations fluctuate?

(5) *Species interactions:* Does the presence of one species hinder or enhance the survival or reproduction of another species?

(6) *Aquaculture:* Can we insure domesticated crops of desired species?

(7) *Enhancement:* Can we release fish eggs and larvae into the sea and thereby increase stocks?

(8) *Pollution:* Do pollutants affect fish populations through their effects on fish eggs and larvae?

(9) *Subpopulations:* Do more than one stock contribute to a fishery?

(10) *Production:* How many fish can a body of water produce and support?

FIGURE 5.—Milner B. Schaefer, about 1970.

Distribution

Sette did one of the first, if not the first, comprehensive ichthyoplankton surveys off the U.S. east coast to study the Atlantic mackerel *Scomber scombrus*. His plan for the Pacific sardine, in modified and extended form, has been continued for 40 years. Figure 6 indicates the use of the ichthyoplankton survey off California and Baja California to assess the distribution of a population and how it changes with time. In recent years, the Southwest Fisheries Center has done a finely spaced egg survey which gives an even clearer idea of how spawning ranges change, sometimes coincident with a major environmental event like the 1983 El Niño, a warming of the Pacific over a vast area (Figure 7). Charts of these distributions in California waters have been published in atlases (Kramer and Ahlstrom 1968; Ahlstrom 1969; Kramer 1970; Ahlstrom and Moser 1975) and in many other publications. We know now that when the Pacific sardine population was on the brink of collapse, the remainder of the population retreated into the Southern California Bight, making the remnants even more

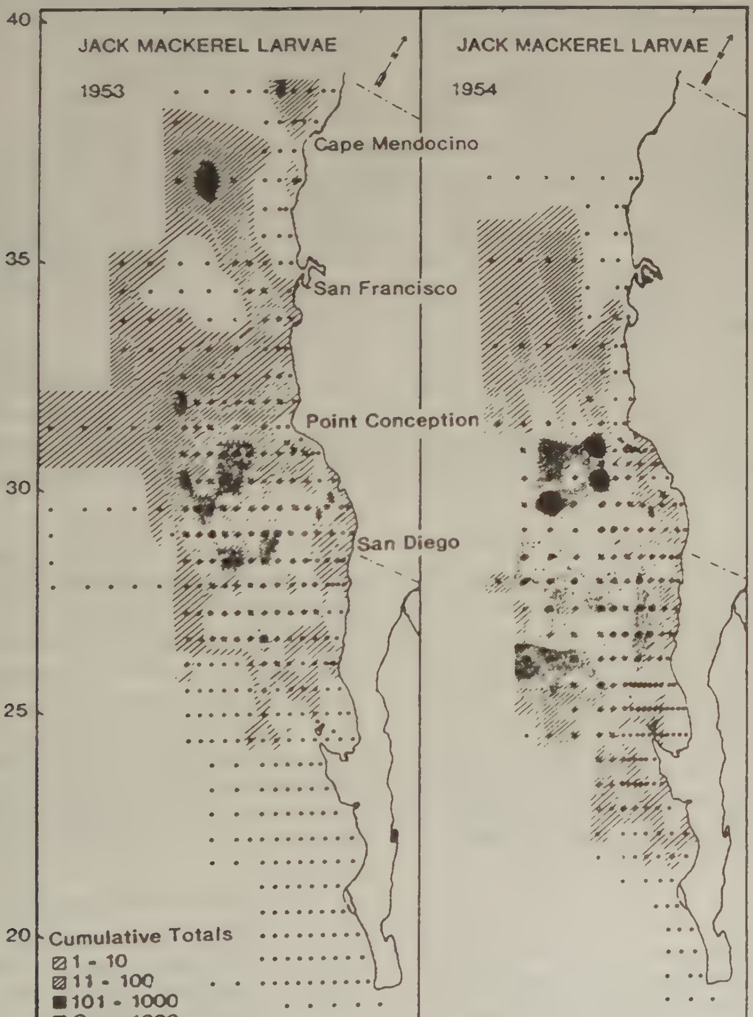
JACK MACKEREL LARVAE
1953
JACK MACKEREL LARVAE
1954
Cape Mendocino
San Francisco
Point Conception
San Diego
40
35
30
25
20
115
110
Cumulative Totals
▨ 1 - 10
▨ 11 - 100
■ 101 - 1000
■ Over 1000
• Stations occupied

FIGURE 6.—Distribution of larval jack mackerel *Trachurus symmetricus* off California, 1953 and 1954. Data are larvae per standard tow.

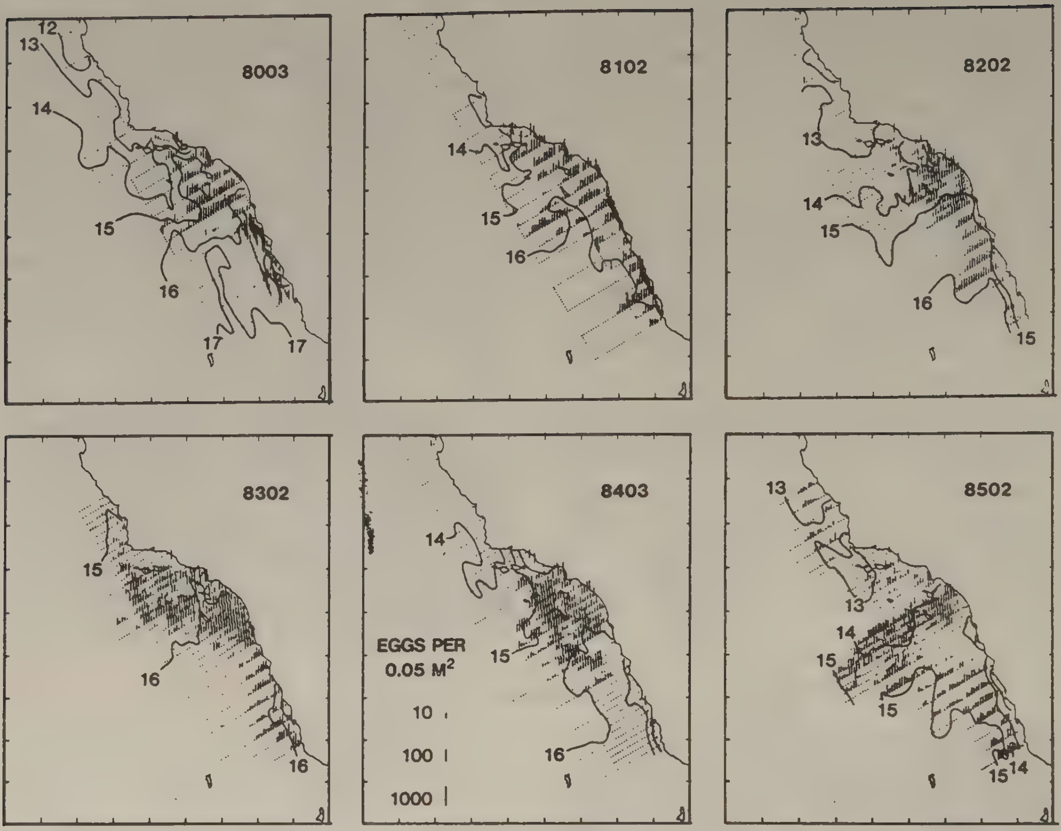

FIGURE 7.—Egg distributions for northern anchovy *Engraulis mordax* off California during February (02) or March (03) 1980–1985. Dots represent sampling stations; surface isotherms are in °C. (From Fiedler et al. 1986.)

vulnerable to fishing (Murphy 1977). The Peruvian anchovy anchovetta *Engraulis ringens* exhibited this same behavior just prior to its collapse (Valdivia 1978).

Paul Smith, Geoffrey Moser and Larry Eber are taking the distribution information much further. Using CalCOFI data from 7 years of intensive sampling, they have analyzed changes in the distribution and abundance of major components of the larval fish assemblage off California and Baja California in response to dramatic changes in oceanographic conditions.

Biomass Estimation

Several marine scientists have used the number of fish eggs or larvae to estimate the spawning biomass of commercial species in the sea (e.g., Saville 1964). The difficulty has always been with the assumption that the number of larvae or eggs is proportional to the abundance of females spawning them. In our laboratory, in common with other fisheries laboratories, we have sought an ichthyoplankton method which would be more precise and with which we could assign errors to every biological parameter. We devised such a method for the northern anchovy, which we call an egg production method (Lasker 1985). Briefly, the idea is to encompass the spawning habitat of the population and to sample about 1,000 times within the habitat with a small, rapidly retrieved plankton net (Figure 8). The eggs caught are then related to female fecundity and the frequency of spawning (Figure 9). That is an all-too-brief characterization of a method that takes 40 d of ship time, retrieval of anchovy eggs from plankton samples, staging and aging of the eggs in the laboratory, histological preparation and examination of the female gonads, and mathematical analysis of the data. The advantages of the method are that no assumptions are made about the biology of the fish and it takes 100 fewer days of ship time than our normal larval survey. This technique is

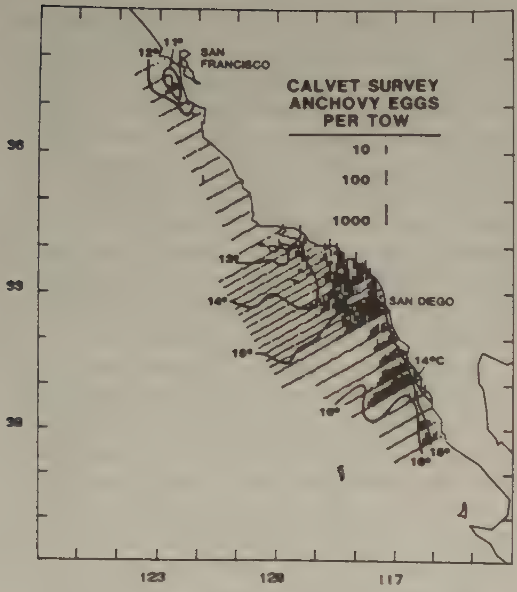

FIGURE 8.—An egg survey for northern anchovy biomass assessment off California in 1982. Surface isotherms (°C) are superimposed on the egg distribution. (From Picquelle and Hewitt 1983.)

now being applied to a variety of fish stocks including the Peruvian anchovetta, the North Sea sprat *Clupea sprattus*, the *Sardinella* off Brazil, and the Pacific sardine, and a program is planned for the Spanish sardine *Sardina pilchardus*.

$$B = \frac{k^1 k^2 P W}{RFE}$$

B	SPAWNING BIOMASS
k^1	SURFACE AREA OF OCEAN OVER WHICH P IS ESTIMATED (units of 0.05 m^2)
k^2	CONVERSION FACTOR FOR GRAMS TO SHORT TONS
P	DAILY EGG PRODUCTION (eggs per 0.05 m^2)
W	AVERAGE WEIGHT OF MATURE FEMALES (grams)
R	SEX RATIO (fraction females based on weight)
F	SPAWNING FRACTION (fraction of mature females that are day-1 post-ovulatory)
E	BATCH FECUNDITY (eggs per mature female)

FIGURE 9.—Equation and parameters for the egg production method of estimating the biomass of spawners (Lasker 1985).

Species Identification

The ichthyoplankton survey had its origin in the work of the Norwegians, English, and Germans at the end of the 19th century. Notable in using plankton nets for determining what plankton were present were Hensen (1895), Schmidt (1909), and Buchanan-Wollaston (1911). In the United States, Sette (1943a) used the survey technique to study the occurrence of Atlantic mackerel off New England from 1927 to 1932. As I have said, it was Sette who outlined the survey program for California, but it was Ahlstrom who honed it to such a degree that the California Current now is one of the best characterized for fish species in the world. These studies were unique for their time because the surveys covered the habitat of an entire population (the Pacific sardine) and have told us what species were associated with it. From monthly cruises over a 10-year-span, the spawning seasons of the Pacific sardine and many other species were delineated. The other species were identified by the construction of life histories through the technique of demonstrating morphological similarities between growth stages. In the last decade, sophisticated rearing techniques have permitted identification of larvae heretofore unidentifiable. Over 200 species of larvae have been identified in the California Current to date, and another 60 or so have been named to family. Numerous publications on the identification and developmental life stages have appeared from the Ahlstrom–Moser laboratory; recently, the volume "Ontogeny and Systematics of Fishes" was produced by Ahlstrom's colleagues and dedicated to his memory (Moser et al. 1984). The ichthyoplankton survey in the Ahlstrom style has been adopted as a scientific tool throughout the world.

Recruitment

As a fishery problem, the prediction of recruitment is foremost in the minds of fishery scientists. Fishery theory has it that if we could accurately predict recruitment a year in advance for most commercial fishes, management would be that much more precise and risks by the fisherman and processors would be greatly reduced. I leave the economics of that to the economists but I would like to comment on the hypotheses about recruitment, specifically on those that involve the survival of fish eggs and larvae.

Hjort (1926) suggested the "critical period" hypothesis: ". . . those individuals which at the very moment of their being hatched did not succeed in finding the very special food they wanted would die from hunger. . . . in other words the origin of a rich year-class would require the contemporary hatching of the eggs and the development of the special sort of plants or nauplii which the newly hatched larva needs for its nourishment." Hjort suggested this hypothesis because the early culture work of the French scientists Fabre-Domergue and Biétrix (1905) showed that larvae of sole *Solea vulgaris* (= *Solea solea*) started to look for food even before their yolk sacs were absorbed; if they did not find food right away, they became "anaemic" (as they called it) and died of starvation. This experimental result, when coupled with the observation that good year classes of several different species of fish sometimes coincided in the Norwegian fisheries, suggested the "critical period" concept to Hjort (1914).

Sette's work did not support the critical-period concept for first-feeding Atlantic mackerel larvae. He found that the greatest mortality occurred late in the larval period, when the animals were about 9 mm long or about 1 month old. But laboratory work on sardine, anchovy, and herring larvae seemed to give results similar to what Fabre-Domergue and Biétrix found with sole larvae, and the testing of the Hjort hypothesis continues to this day.

Fishery scientists are convinced that at least two processes must prevent fish from surviving to a fishable size: starvation and predation. A lot of effort has been expended in recent years trying to decide which is more important and whether the conditions that cause one or the other can be predicted. As an example, my own work showed that food for first-feeding northern anchovy larvae was highly variable in the environment, and, at least in the Southern California Bight, was restricted to nearshore areas (Lasker 1975). Laboratory experiments by my colleagues (Scura and Jerde 1977) indicated that these larvae could not or would not eat diatoms or microflagellates and relied on dinoflagellates or micronauplii in their immediate environment. Furthermore, as aquaculturists know, even foods which are readily ingested do not necessarily support growth and survival. Work off California showed that there was also a threshold number of food particles which had to be in the larva's immediate surroundings before it could be assured a meal. When these facts about the first-feeding larva's needs and behavior are considered, prediction of survival becomes a much more complicated matter because the measurement of all of these factors over a spawning season is a formidable task.

The argument about density-dependent and density-independent recruitment has also occupied fishery biologists. Those believing in density dependency say that we have to take into consideration the number of fish in the population, the number of eggs spawned, and how these numbers have an effect on the number of fish that finally survive. Those convinced that density-independent effects are the most important have ample evidence to show that even unfished populations undergo wide variation in population size, hence recruitment. Hjort also recognized that sometimes very small fish populations could give rise to very strong year classes and in, recent times, we have the examples of the Japanese and Chilean subspecies of Pacific sardine, the North Sea Herring *Clupea harengus harengus*, the chub mackerel *Scomber japonicus* in California, and many others (Figures 10, 11).

The environment seems to regulate the food available for first-feeding northern anchovy larvae. Stable ocean conditions favor aggregation of suitably sized food organisms so that above-threshold numbers of food particles become available to the larvae. I found that when a strong

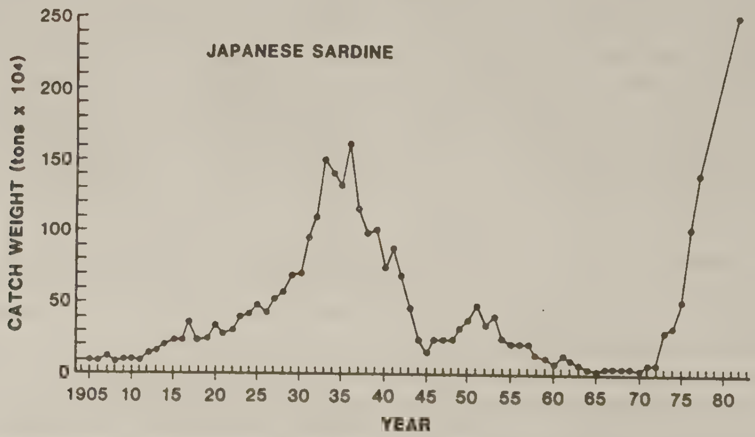

FIGURE 10.—Catches of Pacific sardine off Japan, 1905–1981. The 1984 catch was 420 × 10^4 tonnes.

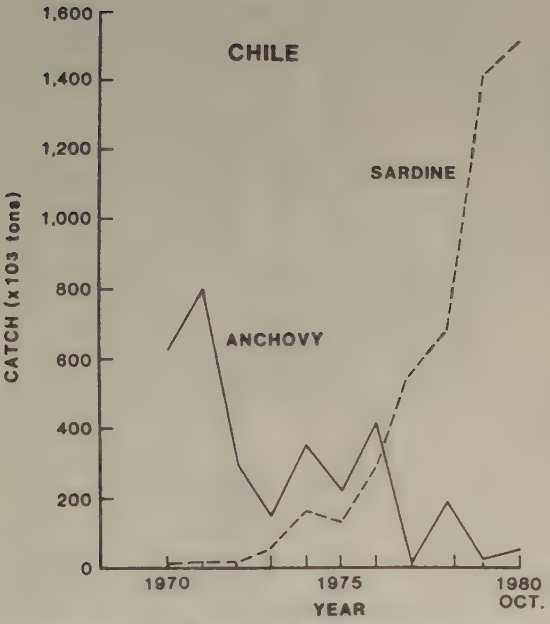

FIGURE 11.—Catches of Pacific sardine and anchovetta off Chile, 1975–1980.

storm or strong upwelling came along, food for the larvae would be dissipated and diluted, making it impossible for first-feeding larvae to find enough food to survive (Figure 12) (Lasker 1981). O'Connell (1976) developed histological criteria by which he could detect starvation of northern anchovy larvae, and he applied these criteria to the estimation of starvation of larvae in the ocean (O'Connell 1980). A reexamination of his data by Theilacker (1987) showed that 35–46% of the first-feeding northern anchovy larvae died from starvation each day. Theilacker (1986) also showed histologically and morphologically that first-feeding jack mackerel are mostly starving in an oligotrophic part of the species' spawning habitat (Figure 13). Close to islands, evidence of starvation drops off considerably; in this case, we must invoke predation as the main cause of mortality (see also Hewitt et al. 1985).

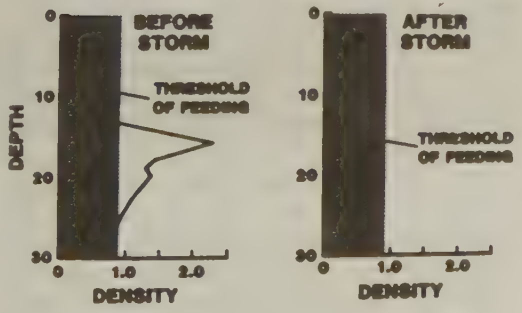

FIGURE 12.—Effect of a storm on the vertical density of particles needed by first-feeding northern anchovy larvae. (From Lasker 1975.)

As far as northern anchovies off California are concerned, it is clear that the kind of food available is of paramount importance too. We have demonstrated that a particular dinoflagellate, *Gonyaulax polyedra*, was the dominant food available to first-feeding larvae in 1975 but, in the laboratory, the larvae could not survive on it (Lasker 1981). That year was an interesting one. Primary production in 1975 was far higher than in any previous or subsequent year but it produced one of the worst year classes of 20 consecutive ones measured. Upwelling brought in diatoms after sweeping out the bloom of *Gonyaulax polyedra*, but diatoms are not eaten by northern anchovy larvae.

The starvation idea also is supported by a modeling study (Lasker and Zweifel 1978) and an energetics study with northern anchovy larvae by Theilacker (1987). Both indicated that the density of food organisms in the sea must be higher than the usual density of nauplii, so the smaller, more dense aggregation of particles (e.g., dinoflagellates) must be the main supply of food for these fragile larvae. When the environment does not cooperate, a poor year class seems inevitable.

The importance of starvation in larval recruitment seems to vary among taxa, however. Houde (1987, this volume) distinguished between anchovy-like species and cod-like species and concluded that the mechanisms for survival and recruitment are different for each group. May (1971b) discovered that larvae of California grunion *Leuresthes tenuis* could withstand up to 20 d of food deprivation after hatching, and concluded that starvation could not be a factor in their mortality in the sea. Recruitment thus depends on a species' behavioral and physiological response to the biotic and abiotic environment, and that generalities with respect to recruitment mechanisms cannot be made. Each species (or species group) needs to be examined separately, and undoubtedly different mechanisms will be found that determine recruitment.

The predation aspect continues to be an intriguing one. Can we get some quantitative fix on recruitment if we know the number and kinds of

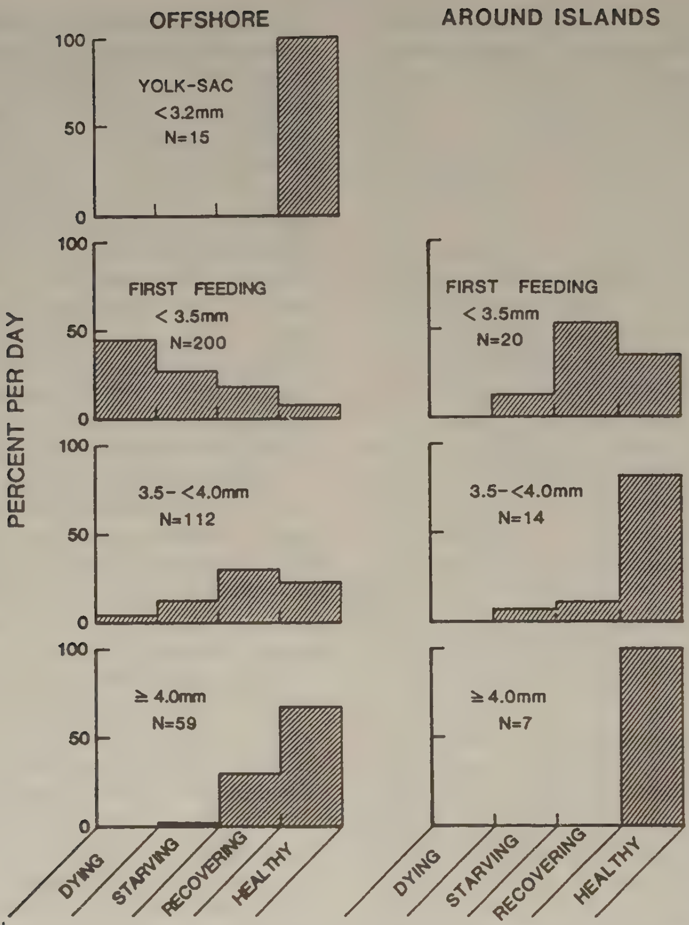

FIGURE 13.—Mortality, starvation, and survival of developing jack mackerel larvae off California. (From Theilacker 1986.)

predators on fish eggs and larvae? Hunter and Kimbrell (1980) have shown that adult northern anchovies feed on northern anchovy eggs and probably the larvae as well. Many other authors have shown how vulnerable fish larvae are to invertebrate predators (Lillelund and Lasker 1971; Theilacker and Lasker 1974; Bailey 1984; Purcell 1985) but we have no tool yet that would allow us to quantify the effect of these predators. An immunoassay technique to detect the degree of euphausiid shrimp predation on yolk-sac larvae has just been developed by Theilacker et al. (1986). The field data are very promising, and this may be what we need to solve the quantitative aspect of predation. Something like this approach is certainly needed now for postyolk-sac larvae.

Our growing expertise in calibrating and reading the ages of larvae and juveniles from the daily rings on otoliths has opened some new avenues to study recruitment of larvae. The important paper by Methot (1983) showed us how we might correlate survival and mortality of larvae with environmental changes. In essence, Methot showed that monthly larval production over a spawning season could be compared to the birthdate frequency of juveniles, i.e., the surviving recruits. For those months in which most survivors had hatched, correlations can be sought with specific events in the environment (Figures 14, 15). It is the first time we have been able to analyze events within a spawning season, rather than averaging variables over an entire spawning season. This idea forms the basis of an international program called SARP, the sardine–anchovy recruitment project, an initiative of the Intergovernmental Oceanographic Commission and the United Nations Food

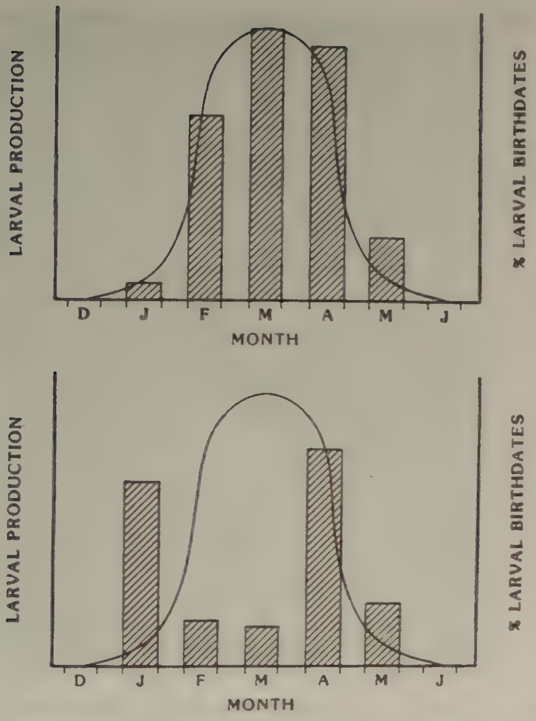

FIGURE 14.—Generalized curves of northern anchovy larval production over a spawning season off California, and distributions (bars) of birthdates of surviving juveniles. The top panel shows the birthdate distribution that would occur if there were no major environmental perturbations during the spawning season. The lower panel shows the distribution that might occur if environmental factors affected survival at various times during the spawning season.

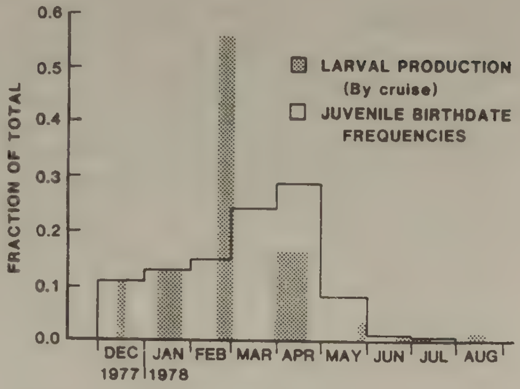

FIGURE 15.—Methot's (1983) actual data for larval production and birthdates of juvenile northern anchovies during the 1977–1978 spawning season off California.

and Agriculture Organization under the International Recruitment Program (IREP).

To summarize this recruitment section, it seems to me that we are on the threshold of making great strides in understanding how fish larvae are controlled by their physical and biotic environment and to quantify the roles that environmental factors play in recruitment. I think Hjort would be pleased with the progress made in the last 15 years, but he would also admonish us because the definitive test of the critical period hypothesis has not yet been made. At the very least the SARP initiative may be the way to accept or reject the "critical period" hypothesis for anchovies and sardines. We have a very long way to go to do the same for the other important commercial species.

Species Interactions

Competition is extremely difficult to observe in pelagic and benthic systems. We know that there is a body of literature on competition for habitat among adult fish, particularly on coral reefs, but how can fish eggs and larvae help us decide whether and to what degree competition occurs? First, one has to have some indication that there is a reciprocal relationship between species; then one can proceed to an analysis of causal mechanisms. As an example, MacCall (in Lasker and MacCall 1983) studied Pacific sardine and northern anchovy scales in anaerobic sediment cores collected from the Santa Barbara Basin, California. He found that northern anchovy scales were smaller when sardine populations were large and larger when sardine populations were small. This kind of presumptive evidence suggests a competition for food among the adults. Does such a competition between species occur in the larval stages?

The CalCOFI data base lists and enumerates the fish larvae of myctophid species, some of which spend their entire lives in the dark and are by necessity carnivorous. Some of these populations are enormous by number if not by biomass and must exert great predation pressure on pelagic fish larvae of all kinds. Some fish larvae, e.g., those of chub mackerel, can eat northern anchovy larvae handily in laboratory tank environments. Competition between individuals of different species for food somehow seems unlikely because fish larvae are usually such a small component of the plankton, but what do we really know? Not much. I think it is clear that this is an area of research that requires much more attention and may have very important implications for multispecies management of commercial species.

Aquaculture

I think the evidence is very good now that aquaculture is a proven technology for a variety of organisms and is paying off in real money for various carps and tilapias, striped mullet *Mugil cephalus*, madai *Pagrus major*, black porgy *Acanthopagrus schlegeli*, European bass *Morone labrax*, and a host of others, but there are many species which have defied propagation and culture. It is interesting to read the journals devoted to aquaculture. Papers on fish larvae abound, and techniques for raising particular larvae are outlined in great detail. The challenge to early life history scientists is to reduce mortality and insure rapid growth of the egg and larval stages of those species that are desirable for human food and commerce.

The use of the rotifer *Brachionus plicatilis* for larval food was introduced in Japan in 1965 and was a breakthrough for fish rearing, although the species originally was considered a noxious zooplankter in eel culture ponds (Hirano 1969; Hirata 1979). *Brachionus plicatilis* has succeeded almost everywhere it has been tried with marine species. In La Jolla, we have used a clone isolated from the highly saline inland Salton Sea (Theilacker and McMaster 1971) to rear northern anchovy larvae; nauplii of the euryhaline crustacean *Artemia salina* have probably been used even more as a larval fish food and also with notable success (May 1971a). Copepods are very desirable for this purpose but culturing them in appropriate quantities is a more formidable problem.

Aquaculturists would be the first to say that their task is not easy and that the road to success is filled with obstacles, but we have seen remarkable progress in fish rearing during the last three decades. This has been accomplished in great part by academic and applied scientists who have had an interest in determining the behavior and the fastidious environmental and food requirements of fish larvae in freshwater and marine systems. I was an early skeptic, but I am convinced now that the culture of marine fishes has seen, and will continue to see, some real successes such as we have had with freshwater species.

Enhancement

One of those areas of rearing that needs particular attention is the trend toward enhancement of natural stocks. This leads us back in time to the work of the first Administrator of the U.S. Commission of Fish and Fisheries, Spencer F. Baird (Figure 16). In 1871, Baird persuaded Congress to create the commission and then willingly accepted the charge of countering the decline of fish off southern New England. The next year, he was given the charge of artificially propagating fish to replenish and restock depleted freshwater and marine areas. There were some successes with, for example, various salmonids and common carp *Cyprinus carpio*, and, in 1878, a major program was started with marine species. Baird did not think that there would be much success in the open sea but he was convinced that there would be some impact in local coastal areas, such as from the several million larvae of Atlantic cod *Gadus morhua* that were released into Gloucester harbor, Massachusetts. There was little evidence of any effect, however. I am not sure we have yet learned the important lesson, now over 100 years old, that any attempt to enhance natural systems requires us also to determine what proportion of stocked animals survives. The failure to do this was really the undoing of the marine enhancement program Baird had so laboriously erected (Allard 1978).

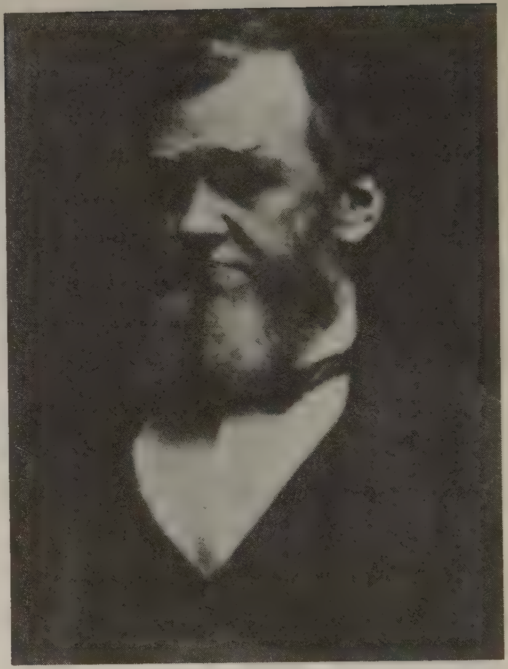

FIGURE 16.—Spencer F. Baird, first U.S. Commissioner of Fisheries. (From Allard 1978.)

In the early years of the Fish Commission, Baird was an active participant in the American

Fish Cultural Association, which, after 1884, was known as the American Fisheries Society. Thus the Early Life History Section of the American Fisheries Society has important historical roots.

Pollution

Surprisingly, we do not yet have a larval fish analog of the laboratory white rat. With all the rearing of larvae going on at present, one would have expected that some larval fish would have made the perfect test organism for pollutants. In 1965, when the Santa Barbara, California, oil spill occurred, I used northern anchovy larvae as test organisms in the laboratory to see if the dispersant used by the oil companies was in any way toxic. It was no surprise that the dispersant was highly toxic to larvae in concentrations as low as 2 mg/L (Anonymous 1969). I then received funds to see if northern anchovy larvae could be used to evaluate other pollutants. The work resulting from that program showed that the larvae take up chlorinated biphenyls directly from sea water (Scura and Theilacker 1977). My own agency considered this work a very low priority at that time, however, and it was terminated.

Granmo (1981) reviewed some of the reasons for using fish eggs and larvae in pollution studies, and listed the following. (1) Fish are economically important. (2) Fish eggs and larvae are sensitive to pollutants. (3) It is relatively inexpensive, quick, and easy to run toxicity tests on fish larvae. (4) We know a lot about fishes. In my opinion, there is another reason: fish eggs and larvae may be the key stages in determining the magnitude of fish populations.

What has eluded fishery scientists is some determination of how populations of fish are affected by pollutants. This question should be central to most of the work going on in lakes and the sea, but few studies are aimed in that direction. Currently, in my own laboratory, Michael Prager and Alec MacCall are looking for correlations between historical trends in fish stocks (as indicated by collections of fish eggs and larvae) and contaminant inputs into California coastal waters. To what extent the mortality of fish eggs and larvae might be involved in these correlations requires field experiments no one is really ready to do, yet it is most likely that it is these sensitive stages of development which bear the brunt of ocean and lake pollution.

Subpopulations

Fishery managers always want to know whether a fishery is based on one stock or several. What can fish eggs and larvae tell us about contiguous populations which are close to one another but genetically separate? Does it make sense to use these developmental stages when the adults are available for analysis? I think not, but the ease of capturing the spawn provides genetic material when it is virtually impossible to capture the adults—for example, before a fishery is initiated on a species whose adults live in deep waters but whose eggs and larvae occur at or near the surface.

In 1962, I had the opportunity to work with Blaxter and Holliday on larvae of Altantic herring. My introduction to this species was in Kiel, where Gotthilf Hempel had arranged for me to collect some larvae. I was astonished to find that newly hatched Atlantic herring larvae were only about one third the size at Kiel that they were in the North Sea. Clearly, this species has evolved remarkably different subpopulations within a few hundred kilometers of each other.

The use of larvae in subpopulation studies deserves much more attention.

Production

I have spent a great deal of my professional life pursuing an understanding of fisheries production, trying to evaluate the steps in the marine food chain leading to harvestable fish. It took me about 20 years to realize that this is much more difficult than I had naively thought. It will take many more years and much more effort to come to any real conclusions about production dynamics.

In 1969, Ryther published a harvest prediction for marine fisheries. With admittedly rough calculations, incorporating what we knew at that time about primary and secondary production in the sea, the efficiency of transfer through trophic levels, and the productive areas of the world's oceans, he concluded that the potential sustained yield of fish to humans would not exceed 100 million tonnes (Ryther 1969). Eighteen years later, we find that Ryther (considered by fishery scientists the pessimist of his time) gave us a figure which seems grossly optimistic. Today the harvest is barely 70 million tons and increasing at an infinitesimal rate (Figure 17). One must conclude that we have been doing something wrong or that the assumptions we have made, e.g., that the efficiency of nutrient transfer seen in the laboratory can be extrapolated to the sea, are incorrect. My own work has shown that the magnitude of primary production may have little relation to the size of a resultant fish year class

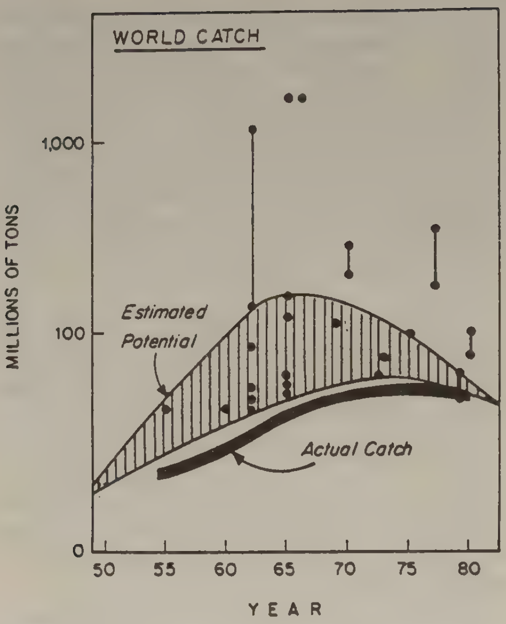

FIGURE 17.—Actual and predicted world fish harvests. (From Darr and Hennemuth 1985.)

(Lasker 1981) and that this discrepancy may be rooted in the behavior and physiology of the larvae. We do not know enough about the inner workings of the larvae of most commercial fish, nor do we know much about how primary production is partitioned among groups of organisms. We now know that most euphausiids (Lasker 1966) and copepods (Cowles and Strickler 1983; Price et al. 1983; Koehl 1984; Strickler 1984) are preferentially carnivores or at least selective feeders just like fish larvae, yet most food chain models are based on their empirically derived filtering rates. Notwithstanding the problems we have with measuring primary production, we have to conclude that the measurement of secondary production is in a very dire condition and requires new insights, new techniques, and a fresh look.

Conclusions

At a student's exam at Scripps Institution, Russ Doolittle, a biochemist, asked if the problem the student had chosen for a doctoral project was a *significant* one. Doolittle explained that, as a student himself, he had worked for professors who seemed to be wrapped up in trivia, trying to find out more and more about less and less. The lesson he was trying to convey was that there are many important problems to be worked on which are just as much fun as any other but carry the added benefit of being important to society as a whole.

In early life history studies of fish we have that added benefit: our work is relevant to fisheries and aquaculture. I have tried to point out some of the significant problems that our laboratory and field studies can address. The papers being given at this meeting illustrate broad recognition of these points. This was not the case 25 years ago, however, and we needed the pioneers I mentioned who had the foresight to persevere with early life history studies. Without them, our work would have been of academic interest only and might never have shown its potential in solving some of society's most pressing aquatic resource questions.

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A history of California rockfish fisheries

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Abstract

Rockfish have been caught off California since prehistoric times. While 60 species are recorded in California waters, less than 20 species make significant contributions to landings by the diverse gears that are used in the fisheries. This paper reviews dynamics in the size and composition of the fishing fleets and landings. Recent events in the fisheries are compared with the history, and important management and research problems of the present are discussed.

History of Landings

Californians have captured rockfish for centuries. California Indians consumed rockfish in prehistoric times (Fitch 1972). Rockfish had attained commercial importance in California by 1875 (Phillips 1957). By the turn of the century, annual landings had reached about 750 mt and there were about 1,500,000 people in the state. Now, with 25,000,000 people, landings of rockfish have increased to 20,000 mt, a 60% gain in landings per capita. The California Department of Fish and Game began compiling fish receipt data in 1916 (Heimann and Carlisle 1970; Figure 1). These data include most landings, but some small landings do not enter normal market channels and are not included.

The landings were fairly stable, generally between 2,000 and 4,000 mt, until the Second World War first interfered with the fishery and then created a large demand. Until 1943, most rockfish were caught by hook-and-line gear; only 5% were landed by trawlers. In late 1943, a boat moved from Astoria, Oregon, to Eureka and used a high-rise trawl called a "balloon trawl" (Phillips 1949). The balloon trawl was very

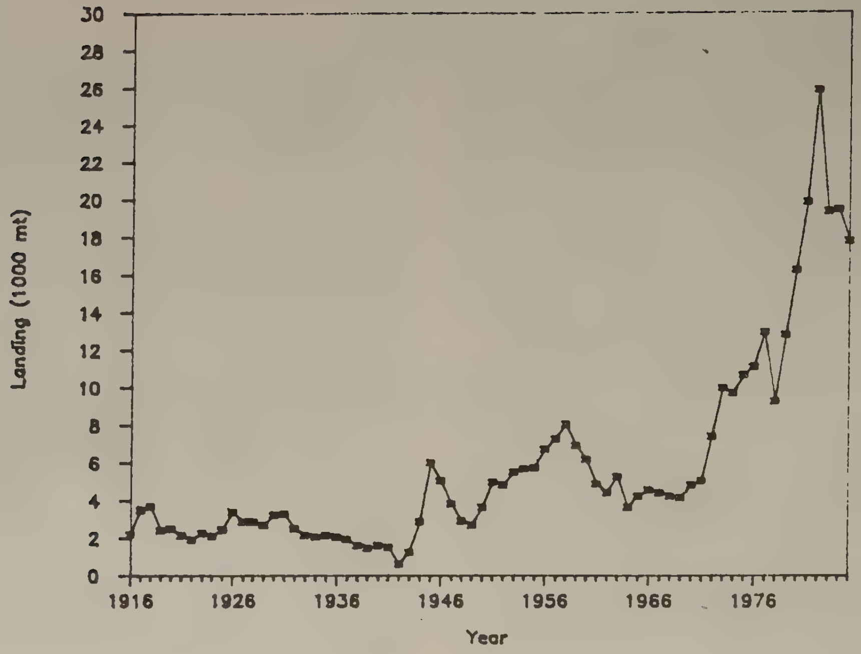

Figure 1. California commercial landings of rockfish, 1916–1985.
Source: 1916–1968 (Heimann and Carlisle 1970),
1969–1970 (Bell 1971),
1971 (Oliphant et al. 1973),
1972–1974 (McAllister 1975, 1976),
1975 (Pinkas 1977),
1976 (Oliphant 1979),
1977–1980 (Frank Henry, personal communication), and
1981–1985 (PacFIN).

effective in capturing rockfish. Use of the balloon trawl spread rapidly and trawl-caught rockfish have dominated the landings since 1944. A peak occurred in landings in 1945 because of the demand from army camps on the West Coast. Landings declined at the end of the war when the camps were phased out.

I did not find explanations for fluctuations in landings between 1950 and 1970. During the past 15 years, landings have increased considerably as the result of better market demand, net design, acoustics, and navigation. Landings peaked in 1982. In that year, many boats from Oregon and Washington fished in northern and central California. These vessels made large landings of widow rockfish (*Sebastes entomelas*) as well as other species of rockfish. In addition to the expanded trawl effort in the 1980's, gill-net vessels also have increased effort.

Since 1983, widow rockfish landings and, to some degree, landings of other species have been constrained by Pacific Fishery Management Council regulations.

The hook-and-line fishery in the early days was fairly primitive. Most trips lasted less than a day and often the crew size was one. Most fishing took place close to port and in water less than 100 fathoms (Scofield 1947). Landings were dominated by black rockfish (*S. melanops*) in northern California, bocaccio (*S. paucispinis*) and chilipepper (*S. goodei*) in central California, and vermilion rockfish (*S. miniatus*) in southern California. After the advent of the balloon trawl, canary rockfish (*S. pinniger*) replaced black rockfish in northern California and bocaccio and chilipepper replaced vermilion rockfish in parts of southern California. Catches of widow rockfish were minor before 1979 when vessels with midwater trawls began targeting on them. In very recent years, bank rockfish (*S. rufus*) have become more important in landings.

Trawl fishery

It is not very meaningful to discuss solely the California trawl fleet, because many vessels fish in more than one state during the year. The fleet is very dynamic. Of the 600 trawlers that participated in the California, Oregon, and Washington fishery for groundfish between 1981 and 1984, only 400 participated in the 1984 fishery. Of the 200 that didn't, records are incomplete for about half (E. Ueber, personal communication). We do know that about 50 sank or burned, 30 fished in other areas or for other groups of fish, and 30 didn't operate because of bankruptcy or other problems.

Most trawl-caught rockfish enter the fresh fish market as fillets. In recent years, widow rockfish, bocaccio, chilipepper, and bank rockfish have dominated the trawl landings. The ex-vessel price of most trawl-caught rockfish is $0.275/lb. The trawl landings of rockfish in California are worth about $10,000,000.

Gill-net fishery

Another important gear for rockfish in southern and central California is the gill net. This gear is prohibited in northern California. Landings by this gear are not as dominated by widow rockfish, bocaccio, and chilipepper as trawl landings are. Yellowtail rockfish (*S. flavidus*) and blue rockfish (*S. mystinus*) are also important.

In 1985, almost 900 vessels were licensed to use gill nets (E. Ueber, personal communication). While I do not have accurate data, probably several hundred gill-net vessels landed rockfish in California.

Our data for California gill-net landings are incomplete, but the catch of rockfish was more than 2,700 mt in 1985. Gillnetted fish tend to be worth more than trawl-caught fish. I estimate that 1985 landings were worth several million dollars to the fishermen. While some gillnetted rockfish are filleted, many enter the market as whole or dressed fish.

A number of problems are associated with the gill-net fishery in California. Besides the usual gear conflicts, there are major incidental kills of seabirds and marine mammals. Because of the problems, there is considerable public support to either ban the gear altogether or severely restrict it.

Hook-and-line fishery

Rockfish are still commercially caught by hook-and-line fishermen in California. While this fishery captures the same species as the other gears, there is a greater tendency to fish for specialized markets such as the Chinese restaurant trade. The brown rockfish (*S. auriculatus*) and several closely related species are preferred for this market. Fishermen receive as much as $3.00/lb for fish in good condition. Sometimes the fish are kept alive until just before cooking.

I don't have a firm estimate of the number of hook-and-line vessels fishing for rockfish in California. It is approximately 300. 1985 landings were about 1,000 mt. I estimate that these landings were worth 1 to 2 million dollars. Most hook-and-line caught rockfish enter the market as whole or dressed fish.

Recreational fishery

Rockfish are very important for recreational fisheries. Besides being good eating, rockfish can be as large as 28 lbs (such as the cowcod, *S. levis*), can be very colorful (such as the starry rockfish, *S. constellatus*), and can be very attractive when viewed underwater (such as the treefish, *S. serriceps*). While catches are usually dominated by one or two species, we have sampled more than 12 species on a single party-boat trip. The variety is appealing to some anglers.

While the California recreational fishery probably is worth more than commercial fisheries of most nations, it is not very well documented. This is because it is difficult to adequately sample recreational landings. Statistics have been collected from the party-boat fishery through a logbook system since 1936 (Collyer 1949, Young 1969). Since 1981, the entire fishery has been sampled by a phone interview and field sampling program (U.S. Department of Commerce 1986).

The party-boat fishery is concentrated in southern California. Prior to the 1950's, rockfish did not support a major targeted fishery in southern California. Anglers preferred the then abundant barracuda (Sphyraena argentea). Barracuda numbers declined and rockfish became very important in the party-boat fishery. The party-boat fishery for rockfish is still minor in northern California.

In 1985, recreational anglers landed almost 8,000,000 rockfish in California (U.S. Department of Commerce 1986). The fish weighed about 4,000 mt. Rockfish comprised almost 1/3 of all recreational fish landed in the state and are the most important group of species. Forty-six species of rockfish were sampled from recreational catches in 1984. However, three species--blue rockfish, black rockfish, and yellowtail rockfish--represent about 30% of the landings. Boat anglers make more than 90% of the landings. Landings from party boats and private boats are about equal.

Economists have yet to agree on how to determine the value of a recreational fishery. One method is to appraise all costs associated with fishing trips. Using this approach, economists estimated that the California recreational fishery for all species is worth about a billion dollars (D. Huppert, personal communication). This is not equivalent to the commercial fisheries values, because there are many factors included in the recreational value not included in the ex-vessel value of commercially landed fish. Still it appears that the recreational value significantly exceeds the commercial value. Agencies recognize this when making management decisions.

Status of fishery

Most stocks of traditional rockfish species in California are at or below the MSY level. Some, such as bocaccio, may be overfished. Present regulations consist of a quota on widow rockfish, 40,000-lb trip limits on commercially caught fish, and a 15-fish bag limit for recreational fish. There are also various gear and area restrictions. The objective of many of the area regulations is to reduce gear conflicts, particularly between recreational and commercial fishermen.

While most of the traditional species are fully utilized, two appear not to be. Recent analysis indicates there is some room for expansion in landings in chilipepper. In addition, bank rockfish landings have increased in recent years. They occupy a habitat that had only been lightly fished previously.

There are two other abundant, lightly exploited species. The splitnose rockfish (S. diploproa) is quite abundant. However, it is a very long-lived species and, while the fishery probably could be expanded some, care is needed in such an expansion because the species could easily become overfished. It is a marginal commercial fish because it produces low fillet yields and is fairly small. Shortbelly rockfish (S. jordani) is very abundant and short-lived. The species probably could support a fishery about the size of the other species combined.

However, it is quite small (maximum size about 30 cm) and must be processed rapidly.

Species targeted by recreational fisheries in southern and central California appear to be fully utilized. Some of the expansion of the recreational fishery has come at the expense of the commercial fishery. Several nearshore species--e.g., black, blue, and yellowtail rockfish--appear to be lightly fished in northern California. Recreational fishing in this area is limited because of the distance from population centers.

Discussion

During historical times the commercial fishery has passed through several phases (Figure 1). Between 1916 and 1947, landings were generally between 2,000 and 4,000 mt. During the Second World War, fishing techniques and markets improved and landings increased to between 4,000 and 8,000 mt until 1971. Since then, techniques and markets have again improved and landings are now about 20,000 mt. The status of exploited species indicates that landings will be between 10,000 and 30,000 mt until other species are harvested. If an increase occurs, it would be a repeat of history. The previous major increases involved changes in the relative importance of species. A future major increase also is likely to involve changes in species composition of landings. Shortbelly and splitnose rockfish are likely to contribute to increased landings. As in the past, improved market conditions are a prerequisite to increased utilization of these two species.

History may also be repeated in the recreational fishery. Significant expansion of recreational landings of rockfish in southern and central California is not likely to occur without reduction of commercial landings.

Management and researchers involved with California rockfish fisheries face several major problems including conflicts between recreational and commercial fisheries. I have already mentioned the gill-net problem. There also appears to be some overcapitalization. The industry, researchers, and managers have been discussing various forms of limited access management, but implementation of such management appears to be years, if not decades, off. Fluctuations in year-class strength cause the fishery to be somewhat unpredictable. Research aimed at this problem is discussed in another paper (Kendall and Lenarz 1987). Researchers are also attempting to develop optimal management strategies that account for the multispecies aspects of the fishery. Finally, monitoring the fishery is quite expensive. We are working on procedures to make sampling more efficient.

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8744

Ageing and Growth of Widow Rockfish

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ABSTRACT

Surface examination of otoliths appears to be satisfactory for age determination of widow rockfish except for large specimens. The results indicate that one ring is laid down per year through age 10. Comparison of surface readings with sectioned readings from difficult-to-read otoliths indicates that surface readings are slightly lower than sectioned readings from such otoliths (3.0 years for males and 2.4 years for females). I recommend that surface readings not be used for males larger than 44 cm and females larger than 47 cm. Data from 2,003 females and 2,184 males were used to estimate the parameters of the von Bertalanffy growth curve.

INTRODUCTION

Previous to this study, a paper by Phillips (1964) is the only publication that develops a growth curve for widow rockfish, *Sebastes entomelas*. His work was based on scale readings and included only a few fish older than 13 years. He did not attempt to verify the accuracy of using scales to age widow rockfish and did not separate sexes. In this study I use otoliths for aging; estimate growth curves for each sex with data from numerous fish estimated to be older than 13 years; and evaluate the accuracy of using otoliths for age determinations.

MATERIALS AND METHODS

Otoliths from sized and sexed fish were made available by the Oregon Department of Fish and Wildlife from samples collected from the commercial fishery in Newport and Astoria; by the Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, from samples collected by observers onboard foreign and joint-venture vessels fishing for Pacific whiting, *Merluccius productus*; and by the California Department of Fish and Game and the Southwest Fisheries Center, Natl. Mar. Fish. Serv., NOAA, from samples collected from the recreational and commercial fisheries of California.

Otoliths were placed in alcohol or water over a black background and examined at 12× for age estimation. Whenever possible, I determined whether the outer edge of the otolith was opaque or hyaline. Such determinations were difficult beyond an age of about 10 years. The criteria used by Kimura et al. (1979) for yellowtail rockfish, *S. flavidus*, were followed for estimating age. However, in contrast to Kimura et al.'s experience with yellowtail rockfish, the anteriodorsal and posteriodorsal regions were usually more easily interpreted than the anterior region. Also, we have found it easier to count from the outer edge to the center of the otolith rather than the reverse, as was usually done by Kimura et al. (1979). Kimura et al. also counted from the outer edge when reading otoliths from older fish. Thick, difficult-to-read otoliths were sectioned using a Buehler Isomet triple-blade saw and read using transmitted light at 50×. Transparent nail mender was used for mounting the otoliths for sectioning and reading. Total lengths were measured for the California samples, while fork lengths were measured for the others. The relationship

$$\text{Fork length} = 6.1635 + 0.9341 \text{ Total length (mm)}$$

was used to estimate fork length from total length. The relationship was estimated by least squares from measurements made of fish captured off California.

The von Bertalanffy growth curve was used to describe growth:

$$\text{Fork length} = L_\infty[1 - e^{-k(\text{Age} - t_0)}]$$

where
L_∞ = theoretical average size at infinite age
k = instantaneous growth completion rate
t_0 = theoretical age when length is zero.

The computer program BGC3 (Abramson 1971) was used to estimate the parameters of the model. Most couplets of age and size used to estimate the parameters were averages of size at age by trimester and sampling area. If sample size from a given area and trimester was less than 10, data from more than one area were combined. Averages for entire years were used for fish older than 13 years because growth is relatively slow at this age and sample sizes were small. If sample size was smaller than 10 for fish older than 15 years, data from adjacent years were combined.

RESULTS

Since geographical location did not appear to have an effect on seasonality of ring formation, samples from all sources were combined for Table 1. The results show that few otoliths have opaque edges during January through April, compared with a large majority during June through November. The marked seasonality of ring formation indicates that otoliths are valid for age estimation of widow rockfish up to about 10 years old. The results are similar to those of Kimura et al. (1979) for yellowtail rockfish, except that the opaque edge appears about a month later in the spring for widow rockfish. Kelly and Wolf (1959) obtained similar results for redfish, *S. marinus*, up to 7 years old from the Gulf of Maine. Westrheim (1973) found that juvenile Pacific ocean perch, *S. alutus*, form one ring per year off British Columbia.

Differences in age estimates between entire and sectioned otoliths are shown in Tables 2 and 3. On the average, age estimates are higher from sectioned otoliths than from entire otoliths of all sizes. There is a tendency for differences in age estimates to increase with size. However, most otoliths were selected for sectioning because they were relatively thick and difficult to interpret. Thus while the tendency is valid for age differences to increase with size, the data in Table 2 are not representative of the true relationship between size and difference. Differences tended to be greater for males than for females. Otoliths from males are thicker for a given size of fish than otoliths from females and are more difficult to interpret. The average difference was only 3.03 years for males and 2.45 years for females, but differences as great as 11 years for males and 14 years for females were observed (Table 3). While these differences seem large, they are small compared with some as great as 50 years found by Beamish (1979) for the relatively slow-growing Pacific ocean perch. In concordance with Beamish (1979), I found the first few annuli adjacent to the focus of sectioned otoliths difficult to interpret. I also agree with Beamish (1979) that structures that I interpreted to be older annuli on sectioned otoliths, and that account for the observations of large differences between estimates from some sectioned and entire otoliths, are often straightforward to interpret and give every indication of being valid annuli.

Data from 2,003 female and 2,184 male fish were used to estimate the parameters of the von Bertalanffy growth curve. When otoliths were sectioned, age estimates from the sections were used. Females and males were treated separately because growth often exhibits sexual differences for rockfish (Beamish 1979; Boehlert and Kappenman 1980; Fraidenburg 1980; Golden et al. 1980; Kelly and Wolf 1959; Kimura et al. 1979; Lenarz 1980; Six and Horton 1977; Westrheim 1973; and Wilkins 1980).

Since Boehlert and Kappenman (1980) found latitudinal differences in growth for *S. diploproa*, growth curves were estimated separately for fish sampled from California and Oregon (Fig. 1). The greatest differences were found for fish less than 7 years old; very few of these fish were caught by the commercial fisheries of Oregon and California, but a significant portion of the California recreational catch is less than 7 years old (Cooperrider 1987). There is a good possibility that the younger age groups that appear in low numbers in the Oregon fishery are relatively fast-growing members

Table 1—Seasonality of ring formation on otoliths of widow rockfish collected off California, Oregon, and Washington, 1978-80.

Month	Number with opaque edge	Number with hyaline edge	Percent with opaque edge
January	4	30	12
February	4	54	7
March	6	33	15
April	3	30	9
May	7	16	30
June	67	9	88
July	215	22	91
August	57	11	84
September	220	1	100
October	230	17	93
November	32	1	97
December	26	11	70

Table 2—Average differences in age estimates between sectioned and entire otoliths of widow rockfish by size and sex.

	Male		Female	
Fork length (cm)	Avg. difference (yr)	No.	Avg. difference (yr)	No.
41	2.5	2		
42	2.4	9	1.3	3
43	3.4	16		
44	3.1	35	1.3	3
45	2.9	33	1.6	7
46	4.0	19	1.1	15
47	2.6	7	1.6	23
48	0.8	4	2.4	43
49	3.0	1	2.9	33
50	0.5	2	2.8	36
51			3.7	20
52			2.5	8
53			2.5	2
			4.0	2

Table 3—Frequency distributions of differences in age estimates between sectioned and entire otoliths of widow rockfish by sex.

Difference (yr)	No. males	No. females
−4	6	1
−3	4	1
−2	2	3
−1	7	12
0	10	25
1	14	30
2	20	39
3	18	34
4	15	17
5	14	9
6	12	11
7	6	6
8	1	2
9	1	1
10	2	2
11	2	1
12		
13		
14		1
Average	3.03	2.45

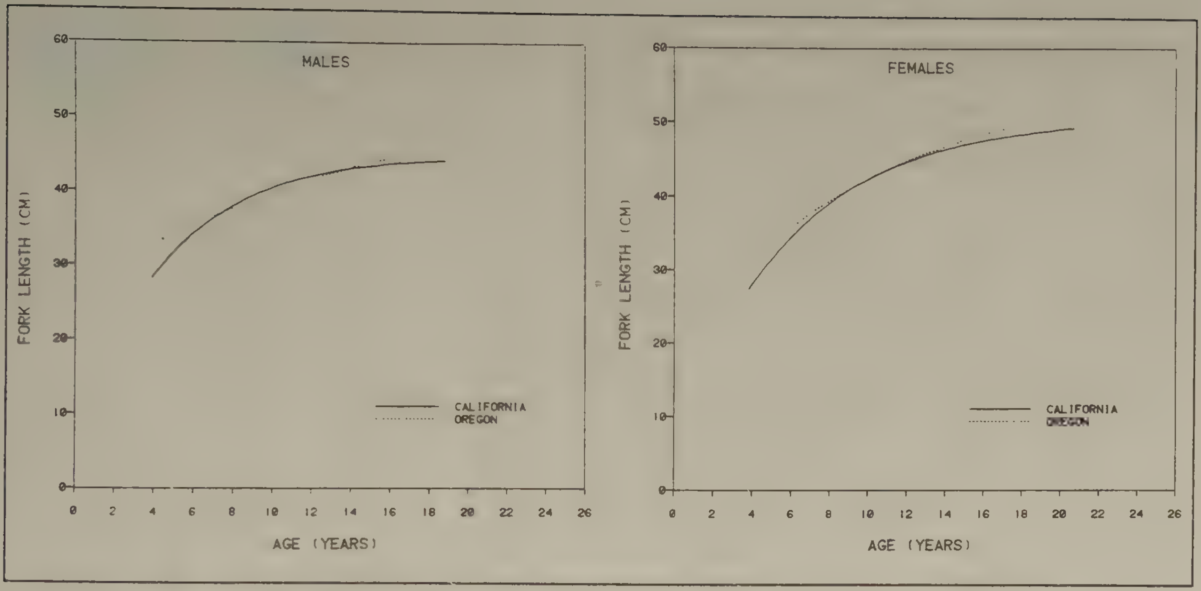


Figure 1—Estimated von Bertalanffy growth curves for male and female widow rockfish caught off Oregon and California.

of their cohorts. Thus, the difference observed in the growth curves could be due to sampling artifacts and not have an underlying biological basis. Consequently, it was decided to combine fish from all areas.

The von Bertalanffy curve provides an excellent description of the growth of females (Fig. 2, Table 4). The relationship was estimated to be

$$\text{Fork length (cm)} = 51.5690(1 - e^{-0.1501(\text{Age(yr)} + 1.4109)}).$$

The estimated growth curve for males is also satisfactory (Fig. 2, Table 5). The relationship is estimated to be

$$\text{Fork length (cm)} = 46.7394(1 - e^{-0.1650(\text{Age(yr)} + 1.9355)}).$$

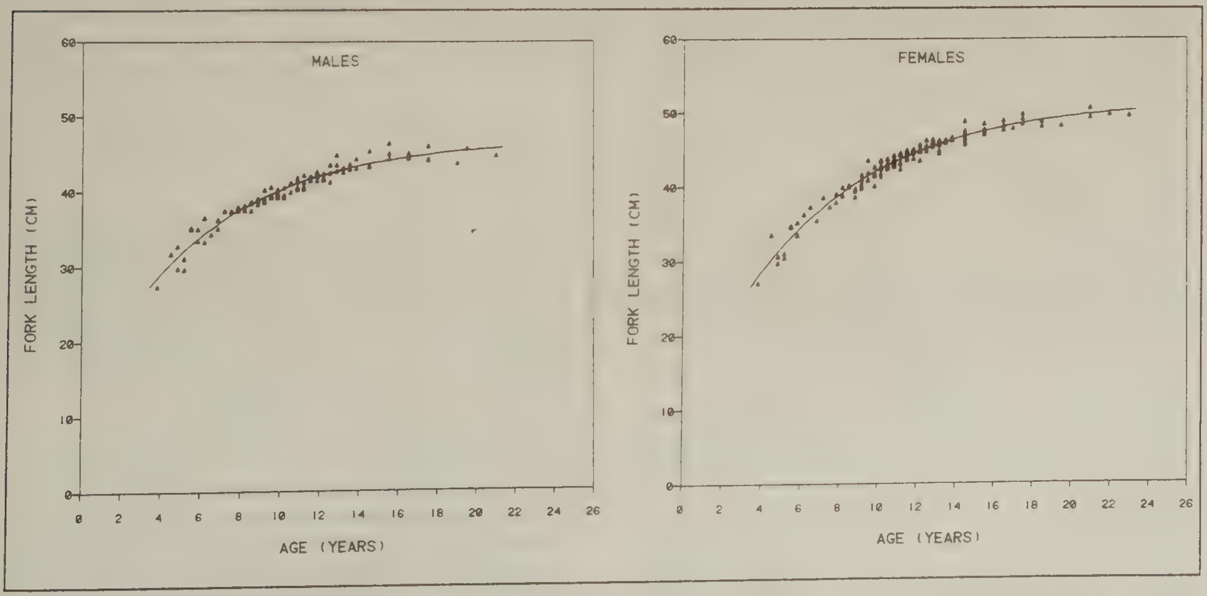


Figure 2—Estimated von Bertalanffy growth curves for male and female widow rockfish caught off California and Oregon, and observations of average size at age.

Table 4—Variables of the von Bertalanffy growth curve for female widow rockfish.

Age (yr)	Number of averages	Estimated average (mm)	Average of averages (mm)	Range of averages Minimum (mm)	Range of averages Maximum (mm)
3.83	1	281	272		
4.50	1	303	336		
4.83	2	314	303	298	307
5.17	2	324	309	306	312
5.50	2	333	348	347	348
5.83	3	342	341	335	353
6.17	1	350	364		
6.50	1	358	374		
6.83	1	366	356		
7.17	1	373	386		
7.50	1	380	374		
7.83	2	387	386	380	391
8.17	3	393	393	383	400
8.50	2	399	402	400	403
8.83	3	405	393	387	398
9.17	5	410	406	398	417
9.50	4	415	419	409	436
9.83	5	420	416	402	427
10.17	6	425	426	415	436
10.50	5	429	429	424	438
10.83	6	434	434	428	442
11.17	6	438	437	424	445
11.50	5	441	442	436	449
11.83	6	445	447	438	450
12.17	5	449	448	436	457
12.50	4	452	454	448	463
12.83	4	455	459	454	464
13.17	6	458	455	445	462
13.50	3	461	462	459	463
13.83	3	463	465	463	467
14.50	6	468	470	457	489
15.50	5	475	476	470	485
16.50	3	481	482	476	489
17.00	1	483	479		
17.50	3	486	492	485	498
18.50	2	490	485	481	488
19.00	1	492	496		
19.50	1	493	482		
20.50	1	496	496		
21.00	1	498	506		
22.00	1	500	497		
23.00	1	502	496		

Table 5—Variables of the von Bertalanffy growth curve for male widow rockfish.

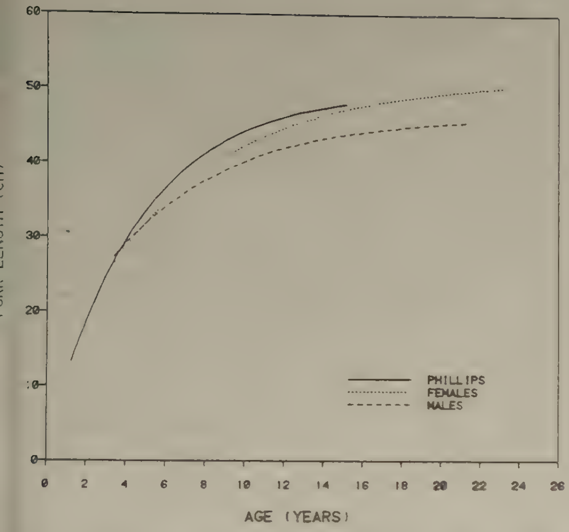
Age (yr)	Number of averages	Estimated average (mm)	Average of averages (mm)	Range of averages Minimum (mm)	Range of averages Maximum (mm)
3.83	1	287	274		
4.50	1	306	318		
4.83	2	314	313	298	328
5.17	2	323	305	297	312
5.50	2	330	352	351	352
5.83	2	338	343	335	351
6.17	2	345	350	333	366
6.50	1	351	343		
6.83	2	357	357	351	363
7.17	1	363	375		
7.50	1	369	374		
7.83	2	374	377	375	379
8.17	3	379	379	375	381
8.50	3	384	381	374	386
8.83	3	388	387	383	390
9.17	4	393	391	385	402
9.50	3	397	398	392	406
9.83	5	400	397	392	402
10.17	4	404	397	392	405
10.50	4	407	408	399	411
10.83	4	411	410	402	418
11.17	5	414	410	403	422
11.50	3	416	418	414	420
11.83	4	419	421	413	426
12.17	4	422	418	415	423
12.50	3	424	424	412	435
12.83	3	426	436	426	448
13.17	2	429	428	425	431
13.50	2	431	433	429	436
13.83	2	433	437	430	443
14.50	3	436	439	432	453
15.50	3	441	452	442	463
16.50	3	445	447	443	450
17.50	3	448	447	440	459
19.00	1	453	436		
19.50	1	454	456		
21.00	1	457	446		

DISCUSSION

A comparison of the growth curves of this study with that of Phillips (1964) (Fig. 3) reveals that Phillips estimated size at age to be larger. The difference may be explained by Phillips' use of scales which are unreliable for age estimates of relatively old rockfish (Kimura et al. 1979; Six and Horton 1977; Westrheim 1973). There is a tendency to underestimate age using scales, and Phillips used back-calculated size at age. An underestimated terminal age could result in size at age being overestimated for some of the subterminal ages of the specimen.

The results for fish 10 years and younger indicate that only one ring per year is laid down. Beyond age 10, the rings appear similar to rings verified as young annuli in younger fish. Otoliths from large fish become thick and difficult to interpret unless sectioned. The first few annuli of sectioned otoliths are difficult to interpret, but interpretation of older rings is often straightforward, since they appear similar to the valid annuli verified through seasonality of ring formation. If accurate estimates of the age of older fish are desired, otoliths should be sectioned in females larger than ~47 cm and males larger than ~ 44 cm. Otolith thickness in fish of a given size varies considerably. Thus it is sometimes desirable to section otoliths from fish smaller than the above guidelines, and sometimes it is not necessary to section otoliths from larger fish.

The estimated values of *k*, 0.1501 for females and 0.1650 for males, are mid-range for rockfish. Values of <0.1 have been reported for Pacific ocean perch (Golden et al. 1980) and splitnose rockfish, *S. diploproa* (Boehlert and Kappenman 1980); and >0.2 for shortbelly rockfish, *S. jordani* (Lenarz 1980), and black rockfish, *S. melanops* (Six and Horton 1977). Since *k* for widow rockfish is well within the range for other rockfish, the population responses to fishing are likely to be about average for rockfish (Adams 1980).



igure 3—Comparison of growth curves estimated for widow rockfish by Phillips .964) and this study. Phillips' data were converted from total length to fork ngth.

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WIDOW ROCKFISH WORKSHOP: Introduction

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INTRODUCTION

This workshop was organized because of the increase between 1978 and 1980 in coastwide landings of widow rockfish, from less than 1,000 mt to more than 20,000 mt, and because of scientists' concern with the lack of knowledge both of the fishery and biology of the species. Most scientists active in research on Pacific groundfish, as well as some members of the fishing industry and fishery managers, attended the workshop.

These proceedings contain the report of the workshop discussion panel, status reports on California, Oregon, and Washington fisheries through 1980, and a collection of seven papers presented at the workshop. The status reports provide an historical perspective of the development of an important fishery. The papers present a fairly complete survey of biological knowledge of widow rockfish, economic status of the fishery, and fishery-independent methods for estimation of abundance. The papers also contain some information developed after the workshop.

Since the workshop, the fishery has matured. Largest landings were made in 1981, when more than 28,000 mt were landed. Maximum sustainable yield (MSY) is estimated to be slightly less than 10,000 mt, and the stock appeared to be at about the MSY level in 1985. The Pacific Fishery Management Council and National Marine Fisheries Service have implemented regulations that have maintained landings since 1983 at approximately the maximum sustainable yield level. Fishery-dependent stock assessments are being made on an annual basis for the Pacific Fishery Management Council. While these assessments are considered to be the best possible with available data, scientists responsible for the assessment have chosen to delay their publication in the formal scientific literature until more data are obtained. However, the stock assessment reports are available from the Pacific Fishery Management Council.

In addition to the papers in this collection, three papers have been published on widow rockfish since 1980. Boehlert, Barss, and Lamberson (1982) estimate fecundity of the species off Oregon; Gunderson (1984) describes the fishery and management actions; and Laroche and Richardson (1981) describe the morphology and distribution of juvenile widow rockfish off Oregon.

During the past decade, the fishery for widow rockfish has developed from a minor fishery to one of the more important on the Pacific Coast. Our knowledge of the biology and dynamics of the species has progressed from minimal to relatively extensive for a groundfish species. It is our intention in preparing this collection of papers to make this knowledge readily available to the scientific community.

CITATIONS

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國立臺灣海洋學院
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第87－01號專刊

漁業生物統計方法

羅黔輝

STATISTICAL METHODS IN FISHERY BIOLOGY

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中華民國七十六年六月出刊

編者序

為迎合中央研究院統計所推廣統計之應用，編者在國科會之支助下，於民國75年2月起在國立臺灣海洋學院漁業研究所授課一學期。課程內容包括基本統計概念和應用統計方法推算海魚（Pelagic fish）早期生活史之成長率和死亡率，並介紹美國西南漁業中心海洋調查和實驗室收集資料之程序。教學材料取自編者在美國西南漁業中心過去五年之數項研究結果整理而成，如有任何錯誤，編者將負全責，並敬請將錯誤函告編者。

漁業學系助教黃娟娟校對、鄭肇雄協助中文修改，呂虹枝同學抄寫全文，編者深表謝意。

羅黔輝

民國75年5月

臺灣　基隆

PREFACE

This course was taught to the first year graduate students of the School of Fisheries at National Taiwan College of Marine Science and Technology during the author's three month stay as a visiting professor, Feb 21 - May 24, 1986. Bulk of the material came from author's research publications in the past five years. The notes include basic statistical techniques applied to fishery problems, and biological parameter estimation procedures for the early life stages of pelagic fish, northern anchovy (Engraulis mordax) in particular.

The text was written in Chinese so that it may be used as a future reference for Chinese fishery biology students and researchers. The notes were first hand-copied by Ms. Horng-Jy Leu and edited by both Ms. Jenny J.J. Hung and Mr. Chao-Hsiung Cheng. The author deeply appreciates their effort and time. For any error found in the text, the author takes full responsibility. The author sincerely thanks the U.S. National Marine Fisheries Service for granting her three month leave, the Institute of Statistics, Academia Sinica, for the sponsorship, and National Science Council of Taiwan, Republic of China, for the funding.

N. Chyan-huei Lo
Keelung, Taiwan, R.O.C.
May, 1986

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一、序　論（ Introduction ）

1.1　統計的目的（ Objective of Statistics ）

統計的目的是從樣本（ Sample ）中取得的資料對母體（ Population ）作一些推論或結論（例如估計、預測或作決策）。

定義：

母體（ Population ）是包括所有具有某種特性的觀察量（ Observation ），這些觀察量可能是可數的（定量的）度量（ Quantitative Measurements ），例如長度、重量、捕獲量，或者是定性的（ Qualitative ），例如性別，標籤與否等。樣本（ Sample ）是實際上的一些觀察量。

如何抽樣和如何分析資料以便從樣本中得到最多的資料（ Information ），這種程序被稱作實驗（ Experiment ），因此統計問題牽涉到：

1. 實驗設計或抽樣程序。
2. 資料收集和分析。
3. 自樣本中獲得的資料對母體作結論。

例 1.1　1965－68，加州漁獵部（ California Department of Fish and Game ）作了幾次海蝦（ Ocean shrimp ; Pandulas jordoni ）的調查。在每次調查中，隨意抽選 150 站，在每一站上拖網 30 分鐘的捕獲量是觀察量，所有可能的捕獲量是母體。樣本平均捕獲量是用來估計（推測）母體的平均捕獲量，海蝦總群量是依據抽樣的資料決定的。

例 1.2　Yuba 河的母鮭魚（ Spawning salmon ）的魚體長是一個母體。如果抽樣一百條母鮭魚並量體長，這一百個體長量度形成一個樣本，可用作估計母體的魚體長。

例 1.3　一位漁民欲知道月齡對捕魚的影響，在一年中，他每月捕魚兩次，一次是在月圓，一次是在新月，每月被歸類於月圓時其捕魚之好與壞，他的資料如下：

	月圓	新月	總次數
捕魚好	七	五	十二

這些資料包括 12 個觀察值。這個試驗的目的是要決定他是應該在那一階段去捕魚或者根本是不須考慮月圓與新月，您認為如何？

1.2　隨機變數（ Random Variables ）和機率分配（ Probability Distribution ）

在前一段所有的觀察量中(所有的樣本裏)都有些不規則或不明的機會因素（Chance factors）參雜在其中。例如在例1.2中如果別的一百條魚被捉，你可能得到與第一百條不同的一百條魚體長。簡單地說，不同的樣本（Sample）雖來自一個母體，它們的觀察量（Observation）會不一樣，爲強調這種觀察量或資料的變化，統計學上用了一個名詞叫作隨機變數（Random Variables = R.V.）來代表所有的觀察量。一個隨機變數是一個數量，從一個觀察到另一個觀察，這個數量可能在變。R.V.有兩種，一種是連續的（Continuous）R.V.，例如魚體重量、魚體長。另一種是離散性的（Discrete）R.V.，例如魚的條數。普通用英文大寫字母X、Y、Z代表隨機變量，小寫x、y、z代表實際上的數量。

既然在樣本之間有這種不規則的變化，我們如何能夠利用樣本的觀察量來對母體下結論呢？這是可能的，只須要有一個持久性的（Long－run）規則性存在。例如擲一個均勻的銅板，若僅丟擲一次，其結果正反是很難預測的，但是如果我們丟擲100次，結果正反出現之次數近乎50－50。

要應用這常規來評估統計試驗，機率理論是非用不可。在任何一種抽樣試驗中（Sampling experiments），總有一套的可能結果（Possible outcomes）或者是隨機變數的可能數字。這一套被稱爲樣本空間（Sample space）。

跟據這樣本空間，可擬定一個數學上的或理論上的模式。它是根據試驗上的假定（Assumptions）和試驗上要測量的假設（Hypotheses）而定的，這種數學上的模式決定樣本空間的各樣本價值，及其機率（Probability），這一套與樣本有關的機率就是機率分配（Probability distribution）。

例1.4　擲一個均勻的銅錢，隨機變數是正面的數量

R.V.	樣本點	機率
X	1（正面）	$\frac{1}{2} = P$
	0（反面）	$\frac{1}{2} = 1 - P$

爲了運用機率模式，我們必須有一些有關如何應用機率之規則。

定義：

一個事件（Event）是一組樣本點（Sample points）卽一種或多種的試驗結果。在擲兩個銅錢的例子裏，正面數量是一個隨機變數（可能的結果是0，1，或者2；樣本點）。正面出現是一個事件，一個或二個正面出現又是一個事件。如果用A和B代表兩個事件：

$A+B=A$ 出現或者 B 出現

$AB=A$ 和 B 同時出現

$\overline{A}=A$ 不出現

例 1.5　一個魚缸有二十條魚

	雄	雌
年齡小於 6 星期	3	9
大於 6 星期	5	3

如果我們隨便捕一條魚（一條魚隨意地被捕；與“有意的”相反），A：此魚是雄的，B：此魚魚齡是小於 6 星期，請計算下列機率：A，B，$A+B$，AB，$\overline{A}$，$\overline{B}$。

機率的幾條規律是符合於相對次數（Relative frequencies）。

規一、如果 A 不發生，$P(A)=0$

二、所有事件機率的總和是 1

三、$P(A)+P(\overline{A})=1$

四、$P(A+B)=P(A)+P(B)$

五、$P(AB)=P(A)P(B)$ 如果 A 和 B 是獨立事件：一個事件的發生不影響另一事件的機率 $P(A/B)=P(A)$

機率理論和統計理論都牽涉及自母體到樣本，機率假定母體是已知的，而來計算某一特殊樣本的機率，統計假定樣本已知，而運用機率來解釋母體。

以下是幾個常用的機率分配函數（Probability distribution functions）：

A、常態分配（Normal distribution）

在自然界中很多隨機變數的分配是像一個鐘形，叫作常態分配。常態分配的隨機變數有兩個參數，一是平均值（Mean；μ），一是變方（Variance；σ^2）。常態分配是以平均值爲中心，兩邊對稱的，它的密度函數是

$$f(x)=\frac{1}{\sqrt{2\pi\sigma}}e^{-\frac{1}{2}\frac{(x-\mu)^2}{\sigma^2}}\qquad -\infty<x<\infty$$

$$\int_{-\infty}^{\infty}f(x)=1$$

$P(X<x_0)=\int_{-\infty}^{x_0}f(x)dx$　任何一個觀察量少於一特殊值（x_0）的機率等於在此曲線之下，直到此點（x_0）的面積，我們寫作 $P(X<x_0)$。大多數統計書籍皆有標準常態分配的 $P(X<x_0)$ 機率表，*i. e.* $\mu=0$，$\sigma^2=1$（看參考書例）。

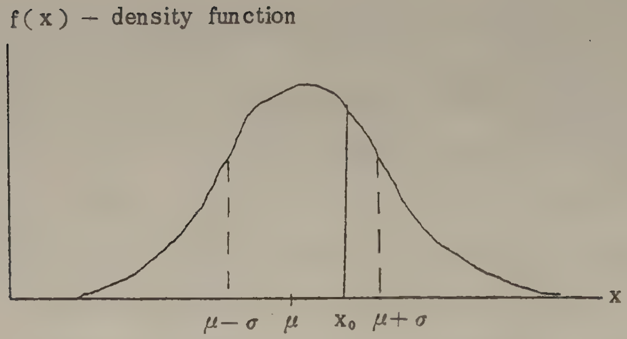


圖 1.1 Normal distribution density function

常態分配 R.V. 之最重要的特徵是 68 ％的數量在 $\mu-\sigma$ 和 $\mu+\sigma$ 之間，95％的數量在 $\mu-2\sigma$ 和 $\mu+2\sigma$ 之間，99.7 ％的數量在 $\mu-3\sigma$ 和 $\mu+3\sigma$ 之間。這些特徵條件在統計推論問題中常常用到。

中央極限定理（ Central limit theorem ; C.L.T. ）：如果獨立隨機樣本取自一個具有平均值 μ 和標準差 σ 的母體，每一樣本包括 n 觀察量，當 n 很大時，樣本平均值 $(\overline{X})$ 將會是常態分配 $(\mu, \frac{\sigma}{\sqrt{n}})$。

此一定理（ C.L.T. ）促使常態分配成爲統計中最重要的機率分配。如果 μ 和 σ 是已知數，n 很大，我們能應用 C.L.T. 來計算樣本平均值小於某一數量的機率。

例 1.6　在一個比較網目大小對海蝦總體的影響中，我們須知道蝦頭胸甲長（ Carapace length ）的分配，假如任何一年齡的頭胸甲長是常態分配。請計算下列各種區間的預期比率：14.5－15.0 mm ，15.0－15.5 mm ，……，18.5－19.0 mm，頭胸甲長平均值是 17.1 mm ，標準差是 0.81 mm 。

Let X = carapace length of ocean shrimp .

$$
\begin{aligned}
P(14.5 < X < 15.5) &= P\left(\frac{14.5-17.1}{.81} < \frac{X-\mu}{\sigma} < \frac{15.0-17.1}{.81}\right) \\
&= P(-3.21 < Z < -2.59) \\
&= P(2.59 < Z < 3.21) \\
&= P(0 < Z < 3.21) - P(0 < Z < 2.59) \\
&= .4999 - .4952 = .0047
\end{aligned}
$$

Then the same is done for the next class interval.

$$
P(15.00 < X < 15.50) = P\left(\frac{15.00-17.1}{.81} < \frac{X-\mu}{\sigma} < \frac{15.50-17.1}{.81}\right)
$$

$$= P(-2.59 < Z < -1.98)$$

$$= P(1.98 < Z < 2.59)$$

$$= .4952 - .4761 = .0191$$

The probabilities of the remaining class intervals are left as homework.

Finally we have

Carapace length interval	Probability or expected proportion
14.50 − 15.00	0
15.00 − 15.50	.02
15.50 − 16.00	.07
16.00 − 16.50	.14
16.50 − 17.00	.22
17.00 − 17.50	.24
17.50 − 18.00	.18
18.00 − 18.50	.09
18.50 − 19.00	.03
19.00 and above	.01

B、二項分配（ Binomial distribution ）

當在標本中的每一個單位可以被列爲具有或沒有一種特徵，例如一條魚是雄的或是雌的；是有標籤的或沒有標籤的；一個人抽煙或不抽煙；一件物品是好的還是壞的，這兩個特徵可以被通稱爲成功或失敗。一個包括有與否特徵的單位就是二項母體（ Binomial population ），如果我們用 1 表示成功，用 0 表示失敗。二項母體就包括 0 和 1 。用 X 代表二項母體的隨機變數， p 是 $X=1$ 的機率， q 是 $X=0$ 的機率， $p+q=1$ ，如果 $X_1 \cdots \cdots X_n$ 是來自一個二項母體的獨立觀察量，則樣本總量 $Y=\Sigma X$，成功總數，就是跟隨二項分配，其參數爲 n 和 p ，或者寫成 $Y \sim B(n, p)$。

二項機率密度函數，是

$$P(X=y) = f(Y=y \mid n, p) = C_y^n p^y q^{n-y}$$

$$= \begin{cases} \dfrac{n!}{y!(n-y)!} p^y q^{n-y} & y = 0, 1, \cdots\cdots n \\ 0 & \text{否則} \end{cases}$$

Y的平均值（μ）和變方（σ^2）是

$\mu = np$ ； $\sigma^2 = npq = np(1-p)$ ； $\sigma^2 < \mu$

下列例題說明如何自一個二項分配中計算機率：

例 1.7 每年打獵季節的第一天只有30％的擁有打獵執照者會被抽出准許打獵，請計算在 5 人中有 4 人被抽的機率。

Solution： $n = 5$ ， $p = .3$

Y = number of people getting drawn

$P(Y=4 \mid n=5, p=.3)$

$= C_4^5 (.3)^4 (.7)^1 = .028$

例 1.8 一家餐館有下列程序來檢查牡蠣，當 10 個牡蠣被隨意選出時，如果二個或二個以上是壞的，此批貨將被拒絕。接受此貨的機率是多少？

1. 如果 5 ％的牡蠣是壞的　　2. 如果 10 ％的牡蠣是壞的

Solution： Y = number of defectives

$n = 10$

(a) $p = .05$

P (accepting the stock)

= P (observing 1 or fewer bad oysters)

$= P(Y=0 \text{ or } Y=1 \mid n=10, p=.05)$

$= P(Y=0) + P(Y=1)$

$= C_0^{10} (.05)^0 (.95)^{10} + C_1^{10} (.05)^1 (.95)^9$

$= .5987 + .3151 = .9138$

(b) $p = .1$

P (accepting the stock)

$= P(Y=0 \text{ or } Y=1 \mid n=10, p=.1)$

$= P(Y=0) + P(Y=1)$

$= C_0^{10} (.1)^0 (.9)^{10} + C_1^{10} (.1)^1 (.9)^9$

$= .348 + .387 = .736$

P (rejecting the stock) = 1 − P (accepting the stock)

$= 1 - .736 = .264$

如果 np 和 n（1－p）大於 5 ，可用常態機率來估計二項分配之機率。

例 1.9　三分之一的魚是雌性的，隨機採樣 30 條魚，計算 10 條魚是雌的機率？

Solution：　Y = number of females

$n = 30$

$p = 1/3$

Using binomial formula, we have

$$P(Y=10 \mid n=30, p=1/3)$$

$$= C_{10}^{30}(1/3)^{10}(2/3)^{20}$$

$$= \frac{30!}{10!\,20!}\frac{2^{20}}{3^{30}} = .15$$

Using normal approximation based on C.L.T. we have

$$P(Y=10 \mid n=30, p=1/3)$$

$$= P(9.5 < Y < 10.5 \mid \mu = 30(1/3) = 10, \sigma^2 = 30(1/3)(2/3) = 6.66)$$

$$= P\left(\frac{9.5-10}{\sqrt{6.66}} < \frac{Y-\mu}{\sigma} < \frac{10.5-10}{\sqrt{6.66}}\right)$$

$$= P(-.19 < Z < .19)$$

$$= 2P(0 < Z < .19)$$

$$= 2(.075) = .15$$

C、卜瓦松（Poisson）分配（稀少事件之分配）

卜瓦松分配是空間（Space）或時間（Time）的一族系（Family）分配，例如在盤中一方格裏的細菌數量，在一單位體積的水中魚卵的數量。更精確些，如果每一單位體積的水中卵數平均值是 λ，則在一單位體積的水中發現 Y 個卵的機率是根據下列公式

$$f(y) = P(Y=y \mid \lambda) = \begin{cases} \dfrac{e^{-\lambda}\lambda^{y}}{y!} & y = 0, 1, 2, \cdots\cdots \\ 0 & \text{否則} \end{cases}$$

Y 的平均值和變方都等於 λ　　即　$\mu = \sigma^2 = \lambda$

例 1.10　如果在一盤中每單位面積的細菌平均值是 2（$\lambda = 2$），發現有 k 個細菌的機率是什麼，$k = 0, 1, 2, 3, \cdots\cdots, 7$，如果 $\lambda = 5$ 呢？

Evaluate　$k = 0, 1, 2, 3, 4, 5, 6, 7$

k	P（Y=k）
0	.135
1	.271

2	.371
3	.18
4	.09
5	.036
6	.012
7	.004

Do the same if $\lambda = 5$.

卜瓦松分配族系和二項分配族系有些相同之處，例如機率增加直到平均值，然後下降，然而卜瓦松分配一般而言有長的右尾，參數、λ，描述（決定）卜瓦松分配的有如二項分配的參數 p 一樣。如果二項分配之抽樣 n 很大，p 很小，$\lambda = np$，卜瓦松分配可以用來約計二項分配，應用卜瓦松分配作爲數學模式來解釋數數分配（ Distribution of counts ）須滿足下列條件：（ P.22 , Elliot 1971 ）

1. 在抽樣地區中，任何一個個體出現在任何一地點的機率是一常數（ Constant ）並且此機率很小（ $p \to 0$ ），因此在任何一地點，個體數目爲零的機率是很高（ $q \to 1$ ）。
2. 樣本單位（ Sampling unit ）的平均個數是極小於樣本單位的最高容量。
3. 在某一地區一個個體的存在不影響發現另一個體的機率，即每一個個體是獨立分別的單位。
4. 樣本（ Samples ）比母體要小 $\frac{n}{N} \to 0$。

第一個條件說任何一個個體，佔據任何一個地點的機會是一樣的，要滿足此一條件，每一個體必須完全地隨機分佈在抽樣地區中。如果某種魚類在抽樣地區中很繁多而擁擠，每一抽樣單位的魚數達到飽和點，則不符合第二個條件，此時二項分配將是比較合適的模式（ $s^2 < \bar{X}$ ）。如果不符合第三個條件，即表示個體不是隨機分配，則卜瓦松分配是不適合的。遷移一個樣本單位會影響到另一樣本單位的機率。但是如果只是母體的一小部份被移出，則其影響很少，因此第四個條件保證自一個試驗到另一個試驗 P 的價值不變。

一個隨機分配（ Random distribution ）常常是須測驗的第一個假設（如果我們不能拒絕隨機分配則用 Poisson 分配其好處是它很簡單，只有一個參數）。運用卜瓦松必須滿足以上四個條件。沒有試驗能證明隨機合乎卜瓦松分配，但只能說隨機假設沒有被推翻。有時雖然隨機假設被接受，但可能有不隨機的成分的存在只是沒有被發現。

重要的環境因素很少是隨機分配的，所以我們只能說不隨機成份未能被抽樣技術發

現而探測出來。

另一關於隨機分配的重要因素是抽樣單位的大小。如果抽樣單位大過於魚團（Clumps），則母體似乎會是隨機分配，因爲魚團多半是隨機分配的，如果樣本單位小於 $0.05\,m^2$，則不隨機多半可能被探測出來，隨機分配隨魚年齡而異。

如果我們不能拒絕隨機分配的假設，我們建議用卜瓦松分配，因爲這是一個簡單模式，尤其是有關計算信賴界限（Confidence limits）。

欲測驗次數分配是否合乎卜瓦松分配，可作下列的統計測驗：

$$I=\frac{\text{樣本變方}}{\text{理論變方（variance）}}=\frac{s^2}{\overline{x}}=\frac{\Sigma(x-\overline{x})^2}{\overline{x}(n-1)}$$

$$\chi^2=I(n-1)=\frac{\Sigma(x-\overline{X})^2}{n-1}\sim\chi^2 \qquad \text{with } (n-1) \text{ degree of freedom}$$

如果 $n>31$，$\sqrt{2\chi^2}\sim N(2\nu-1,1)$

在此 $\nu=n-1$

如果 $\chi^2<\chi^2_{\nu,0.025}$ （$s^2<\overline{X}$） 可試二項分配

$\chi^2>\chi^2_{\nu,0.975}$ （$s^2>\overline{X}$） 可試負二項分配

D、負二項分配（Negative binomial distribution）

如果應用於卜瓦松分配的第一和第三條件不符合，母體的變方（Variance）通常比平均值要大（$\sigma^2>\mu$），母體是由聚集成小團所構成，好幾種數學模式是用來描述這些情況，但是負二項分配是最普遍的一種。

負二項分配是與二項分配相對的（Counterpart），$(-p+q)^{-k}$；$\mu=pk$，$p=\frac{\mu}{k}$ 並 $q=1+p$；$q-p=1$，其主要參數是平均值 μ 和指數 k，變方 $\sigma^2=kpq=\mu q=\mu(1+\frac{\mu}{k})$ $\therefore \sigma^2>\mu$。當 $k\to\infty$，則 $\sigma^2=\mu$，負二項分配就趨近卜瓦松分配。

$\frac{1}{k}$ 是測量多餘的變方或群聚（Clustering）。負二項分配的密度函數是

$$f(x)=\frac{(k+x-1)!}{x!(k-1)!}\left(\frac{k}{k+\mu}\right)^k\left(\frac{\mu}{k+\mu}\right)^x \qquad x=0,1,2,3,\cdots\cdots$$

$$\frac{p}{q}=\frac{\frac{\mu}{k}}{1+\frac{\mu}{k}}=\frac{\frac{\mu}{k}}{\frac{k+\mu}{k}}=\text{成功機率}=\frac{\mu}{k+\mu}$$

Problems:

1. Give some examples familiar to you of a sample and a population.
2. In EX 1.6 use the table of normal probability distribution. Calculate the probability of the remaining class intervals.
3. Tossing a balanced die, the random variable is the number showing in each toss. Write down the probability density function of this random variable.

   Let A be the event of observing an even number
   B be the event of observing the odd number.

   Using the rules on page 6, calculate P(A) P(B) P(A+B) and P(AB).
4. It is beleived that 20% of the fishing violations in San Luis Reservoir get caught during each fishing season. During January through April 1973, 150 violations were simulated, 38 of them were detected. What is the probability of getting such a sample, using both binomial formula and normal approximation? Does this sample support the claim?
5. Restaurant B in Berkeley has the following sampling procedure to check the oysters shipped from the east coast: If 50 oysters randomly selected from the stock are all good, then the stock is accepted; if 2 or more out of thses 50 oysters are bad, then the stock is rejected; if 1 out of these 50 oysters is bad, then 100 more oysters are randomly selected from the stock. If none of the 100 oysters are bad then the stock is accepted, otherwise, the stock will be rejected. Calculate the probability of accepting the stock when there are

   a. 1% bad oysters in the original stock,
   b. .5% bad oysters in the original stock.

Hint, use the rules $P(A+B) = P(A) + P(B)$ and $P(AB) = P(A) \cdot P(B)$.

6. In a capture-recapture experiment, a small portion (p) of the fish population is tagged. When a large amount of fish (n) is sampled, the number of tagged fish caught (Y) approximately follows Poisson distribution with parameter $\lambda = np$. If tagging ratio is .01 and 200 fish are sampled, calculate the probability of getting tag returns equal to 0, 1, 2, 3, 4 and 5.

   Note: Usually P is never known, therefore the sample tagging ratio is used to estimate population tagging ratio, furthermore, to estimate the fish population.

二、統計推論 (Statistical Inference)

2.1 參數推算

一個母體可以用幾個參數來描述，因為通常不可能觀察整個母體，參數的值量是未知數。如何從樣本中取得資料以便計算最佳參數推算是統計目的之一。

對於參數推算有兩種方法，一個是點推算 (Point estimator)，一個是區間推算 (Interval estimator)，例如：測量 100 條魚後，我們說魚體長平均值是 625 mm，這是魚體長平均值的點推算。如果我們說平均魚體長是在 600 mm 和 650 mm 之間，則 (600 mm，650 mm) 是平均魚體長的區間推算。

定義：

一個推算公式 (Estimator) 是告訴我們如何計算推算值，它是根據樣本之資料，例如樣本平均值 $\overline{Y}=\frac{\Sigma Y}{n}$ 是母體平均值之一個推算公式 (Estimator)，它說明一旦樣本到手，如何計算推算值。

A、點推算

如果 θ 是一個參數，其點推算是寫成 $\hat{\theta}$，"最佳"點推算是不偏差的，$E\hat{\theta}=\theta$，它的預期值或平均值是等於 θ，同時它的變方最小。

a、母體平均值的點推算：

母體平均值有好幾種點推算，例如樣本平均值，樣本中位數，樣本衆數，樣本最大數和最小數的平均。在這幾種推算值中，樣本平均值是不偏差的。同時 (當樣本很大時) C.L.T. 使我們能夠陳述有關樣本平均值的機率。

b、母體變方的點推算：

最常用的母體變方的點推算是 $s^2=\frac{\Sigma(X-\overline{X})^2}{n-1}$ 。

如果隨機變數 X 是來自常態分配，則 s^2 是母體變方的不偏差的推算公式。

B、區間推算

一個參數的區間估計通常是指它的信賴區間 (Confidence interval)，在這一段裏，我們將只討論母體平均值的區間推算。

a、如果樣本大小 (Sample size) 大過30，根據C.L.T.，樣本平均值 $\overline{Y}$ 應是常態分配的，其平均值是 μ，變方是 $\frac{\sigma^2}{n}$，因此 95 % 的樣本平均值應介於 $\mu-2\frac{\sigma}{\sqrt{n}}$ 和 $\mu+2\frac{\sigma}{\sqrt{n}}$ 之間，所以

$$P\left(\mu-2\frac{\sigma}{\sqrt{n}}<\overline{Y}<\mu+2\frac{\sigma}{\sqrt{n}}\right)=0.95$$ (圖 2.1)

經過移項，則得

$$p(\overline{Y}-2\frac{\sigma}{\sqrt{n}}<\mu<\overline{Y}+2\frac{\sigma}{\sqrt{n}})=0.95$$

這是說如果我們一直抽樣，並且樣本大小很大，由每一個樣本，計算一個 $\overline{Y}$，則每一個平均值 $\overline{Y}$ 都可用來計算一個區間推算，i.e.，$\overline{Y}-2\frac{\sigma}{\sqrt{n}}$, $\overline{Y}+2\frac{\sigma}{\sqrt{n}}$，大約 95 % 的區間推算會包括原來的母體平均值，任何一個單獨的（樣本平均值）區間推算或包括或不包括母體平均值，只是因爲如果我們不斷抽樣，95 % 的區間推算會包括母體平均值，使我們對區間推算的信賴度是 95 %，一般說來，$1-\alpha$ 信賴區間（c.i.）是寫成

$$\overline{Y}-Z_{\alpha/2}\frac{\sigma}{\sqrt{n}} \quad , \quad \overline{Y}+Z_{\alpha/2}\frac{\sigma}{\sqrt{n}}$$

$Z_{\alpha/2}$ 是常態分配表中的數值，有 $\alpha/2$ 的標準常態變數大於 $Z_{\alpha/2}$，或者寫成 $P(Z>Z_{\alpha/2})=\frac{\alpha}{2}$，$\alpha$ 是顯著水準（圖 2.2）。

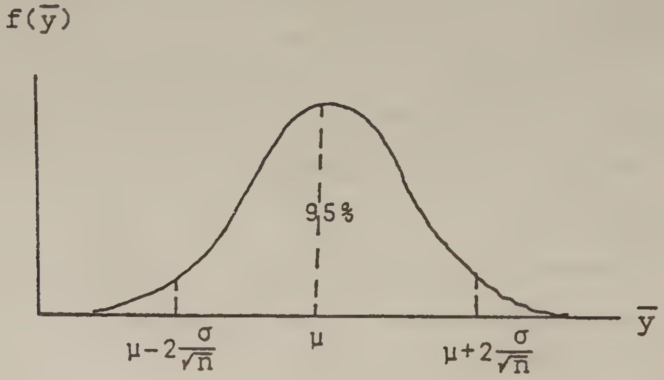


圖 2.1　The normal density function of sample mean ($\overline{y}$) with mean μ and variance σ^2/n. 95% of sample means are between $\mu\pm2\sigma/\sqrt{n}$.

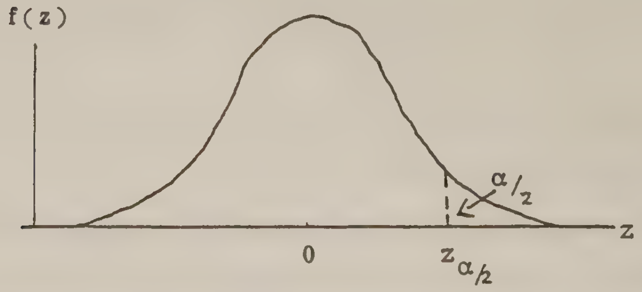


圖 2.2　The density function of the standardized normal random variable, Z. $P(Z>z_{\alpha/2})=\alpha/2$.

如果 $1-\alpha=0.9$ ， 0.9 是信賴係數（Confidence coefficient），$\alpha=0.1$ ，$Z_{\alpha/2}=Z_{0.05}$ $=1.645$ ，90％母體平均值的信賴區間是 $\bar{Y}-1.645\frac{\sigma}{\sqrt{n}}$ ， $\bar{Y}+1.645\frac{\sigma}{\sqrt{n}}$

普通母體變方 σ^2 是未知數，所以用樣本變方 s^2 代替。

例 2.1　1968 年海蝦季節，有一個樣本的海蝦頭胸長度（Carapace length）如下：

Shrimp carapace length (X)	Frequency (f)
15.4	1
15.6	1
16.0	1
16.2	1
16.4	4
16.6	2
16.8	3
17.0	8
17.2	5
17.4	6
17.6	3
17.8	2
18.0	2
18.2	2
18.4	2
18.6	1
18.8	1
19.2	1
20.0	1
20.8	1
21.4	1
21.6	1

計算 95％母體平均值的信賴區間。

Solution： $\bar{X}=\frac{\Sigma fX}{\Sigma f}=\frac{876.8}{50}=17.53$ ……… point estimate

$\Sigma fX^2=15456.16$

$$s^2 = \frac{\Sigma〔f(X-\overline{X})〕^2}{(\Sigma f)-1} = \frac{\Sigma f X^2 - \frac{(\Sigma f X)^2}{n}}{n-1} = \frac{80.5952}{49} = 1.6448$$

$$(17.53 \pm 2\frac{s}{\sqrt{n}}) = 17.53 \pm .3627$$

$$= (17.16, 17.89) \cdots\cdots\cdots 95\% \text{ c.i.}$$

b、如果樣本大小很小（ $n < 30$ ）並且樣本是來自土堆形分配的總體，則 $1-\alpha$ 信賴區間是 $\overline{Y} - t_{\alpha/2,\,d.f.}\frac{s}{\sqrt{n}}$ ， $\overline{Y} + t_{\alpha/2,\,d.f.}\frac{s}{\sqrt{n}}$

$t_{\alpha/2}$ ，d.f. 是來自 t 表，$P(t > t_{\alpha/2}) = \alpha/2$ ，d.f. 是自由度（ Degrees of freedom ）等於 $n-1$ 。

例 2.2　在 1973 Razor 蚌的調查中，在一個高潮的週末，11 位挖蚌人被訪問，他們的蚌殼數量是 18，22，19，20，20，13，22，20，21，20，19，請計算 95 % 的平均值區間估計

Solution:　　X ： Number of clams caught

$$\overline{X} = \frac{\Sigma X}{n} = \frac{214}{11} = 19.45$$

$$s^2 = \frac{\Sigma(X-\overline{X})^2}{n-1} = \frac{\Sigma X^2 - \frac{(\Sigma X)^2}{n}}{n-1} = \frac{4224 - 4163.27}{10} = 6.072$$

$$\frac{s}{\sqrt{n}} = \sqrt{\frac{6.072}{11}} = .743$$

$$t_{.025,\,d.f.=10} = 1.812$$

95 % c.i. for the average clam per digger is

$$\overline{X} \pm t_{.025,\,d.f.=10}\frac{s}{\sqrt{n}}$$

$$= 19.45 \pm 1.812(.743)$$

$$= 19.45 \pm 1.346$$

$$= (18.104, 20.79)$$

C、自二項母體抽樣

應付二項母體，參數 p 是觀察“成功”的機率，通常是未知數須要推算的。樣本中的觀察量 $x_1 \cdots\cdots x_n$ 是自母體中隨機抽選出來的， $Ex = p$ ， $\sigma_x^2 = p(1-p)$ ，樣本比率 $\hat{p} = \frac{\Sigma x}{n}$ 是 p 的最佳推算公式。注意 $\hat{p}$ 就是樣本平均值 $\overline{x}$ （記得 x 是 1 或 0，成功或失敗），所以我們用 $\hat{\sigma}_x^2 = \hat{p}(1-\hat{p})$ 爲 σ_x^2 的點推算。

樣本大時，$\hat{p}$ 是近乎常態分配 $\mu = p$ ， $\sigma^2 = p\frac{(1-p)}{n}$ ， $1-\alpha$　p 的信賴區間是

$$\hat{p}-Z_{\alpha/2}\sqrt{\frac{\hat{p}(1-\hat{p})}{n}} \quad , \qquad \hat{p}+Z_{\alpha/2}\sqrt{\frac{\hat{p}(1+\hat{p})}{n}}$$

例 2.3　1973 年在 San Luis 水庫（ Reservoir ）的違反釣魚法規之研究調查中，模擬 150 件違規事件，其中 38 件被發現，請推算母體中違規比率，並計算 95 %信賴區間。

Solution：　$p =$ the proportion of violations detected each year

$n = 150$

$\Sigma X = 38$

$$p=\overline{X}=\frac{\Sigma X}{n}=\frac{38}{150}= .25$$

$$s_X^2=\hat{p}(1-\hat{p})=(.25)(.75)=.1875$$

$$\hat{\sigma}_{\hat{p}}^2=\frac{\hat{p}(1-\hat{p})}{n}=\frac{.1875}{150}= .00125$$

95 % c.i. for p

$$\hat{p}\pm 2\sqrt{\frac{\hat{p}(1-\hat{p})}{n}}$$

$$= .25 \pm .069 = (.18, .32)$$

如果樣本大小不大，爲 p 建立一個 $1-\alpha$ 信賴區間不是直接了當的事，因爲二項隨機變數是離散性，我們不可能計算一個信賴區間，說是一定等於 95 %，我們首先對於一個已知 p 和 n ，尋找 $\hat{p}_0$ 和 $\hat{p}_1$ ：

$$P(\hat{p}<\hat{p}_0 \mid p)<0.025$$

$$P(\hat{p}>\hat{p}_1 \mid p)<0.025$$

或者　$P(\hat{p}_0 \leqslant \hat{p} \leqslant \hat{p}_1 \mid p) \geqslant 0.95$　（圖 2.3 ，圖 2.4 ）

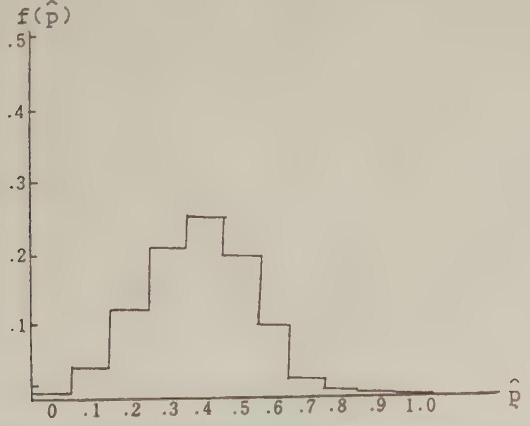


圖 2.3　The probability distribution of sample mean, $\hat{p}$, with mean $p=0.4$ and sample size $=10$.

從不同的 p 值中，計算 $\hat{p}_0$ 和 $\hat{p}_1$ 、 $\hat{p}_0$ 和 $\hat{p}_1$ 形成二個曲線（圖 2.4 ）。

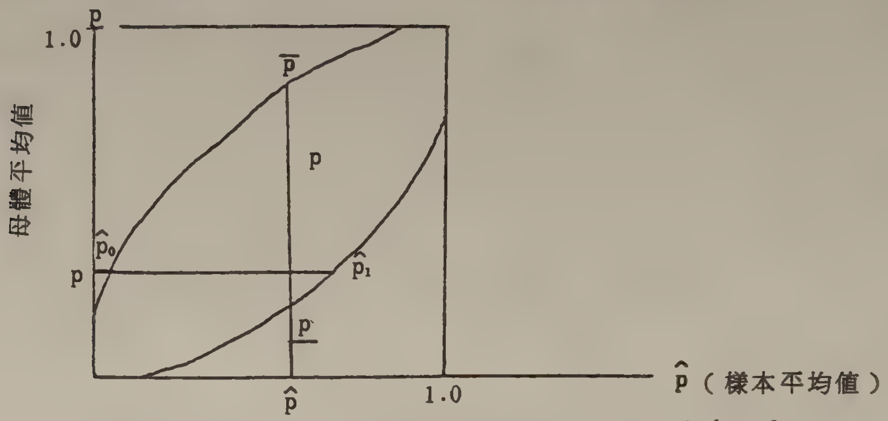


圖 2.4　The confidence interval for population mean, p：($\underline{p}$, $\overline{p}$) based upon sample mean ($\hat{p}$). For the definition of $\hat{p}_0$ and $\hat{p}_1$, see text.

現在我們抽樣，樣本大小（ Size ）是 n ，計算 $\hat{p}_0$ 與 $\hat{p}$ 成一縱線的縱坐標的兩點（ $\underline{p}$ ， $\overline{p}$ ）是大約 95 %的 p 之信賴區間。

運用上圖和二項機率表，我們可以建立 1－α 信賴區間如下：　y 是樣本成功數量

尋找　$\underline{p}$ ：$p(Y > y \mid \underline{p}) \leqslant \alpha/2$　(1)

　　　$\overline{p}$ ：$p(Y < y \mid \overline{p}) \leqslant \alpha/2$　(2)

在二項機率表中，列有 n 和 Y ，找出 p 適合 $\underline{p}$ 和 $\overline{p}$ 的條件。

例 2.4　在一個樣本中有十條魚，三條是雌魚，計算母體比率的 95 %信賴區間。

Solution：　$n = 10$

　　　　　$Y = 3$

Find $\underline{p}$ such that

$$p(Y < 3 \mid \underline{p}) < .025 \qquad \rightarrow \underline{p} = .1$$

$\overline{p}$ such that

$$p(Y < 3 \mid \overline{p}) < .025 \qquad \rightarrow \overline{p} = .6$$

at least 95 % c.i. for p is (.1 , .6)

If normal approximate is used, 95 % c.i. for p is:

$$p \pm t_{\alpha/2,\, d.f.=9} \sqrt{\frac{\hat{p}(1-\hat{p})}{n}}$$

$$= .3 \pm 2.28 \sqrt{\frac{(.3)(.7)}{10}}$$

$$= .3 \pm .33 = (0, .63)$$

2.2 假設檢定（Hypothesis testing）

除了參數的推算之外，假設檢定是統計推理的另一種方法，在這個主題下，先設一個虛無假設，或是針對參數，或是針對隨機變數的分配。在樣本統計量計算之前，先設立一個規則以決定我們接受此假設或否定此假設，所以統計檢定包括四要素：

1. 虛無假設（Null hypothesis ; Ho）
2. 對立假設（Alternative hypotheses ; Ha）。
3. 檢定統計量（Test statistic）
4. 否定範圍和接受範圍（Reject or critical region and acceptance region）

虛無假設 H_0 說明要檢定的假設，所以 H_0 須要有母體參數的假設數值，否定或接受虛無假設的決定在於檢定統計量，此仍從樣本計算出來的，所有檢定統計量或落於否定範圍或落於接受範圍，如果檢定統計量落於否定範圍，虛無假設就被否定了，不然就接受虛無假設。

與假設檢定有關的兩型誤差（Error）：

1. 型一誤差（Type Ⅰ error）：如果虛無假設是對的，但被否定了，則犯“型一誤差”，其機率被稱爲顯著水準（Level of significance），通常用 α 代表。
2. 型二誤差（Type Ⅱ error）：如果虛無假設是錯的，但被接受了，犯“型二誤差”的機率用 β 代表，只在對立假設下的參數數值下計算 β。

否定範圍是決定於顯著水準的數值，並使型二誤差機率達到最小程度。

A、母體平均值的假設檢定

a、大樣本統計檢定

大樣本統計檢定是根據常態分配的檢定統計量，任何檢定程序可以寫成如下：

①虛無假設　$H_0 : \mu = \mu_0$

②對立假設　$H_a : \mu \neq \mu_0$

③檢定統計量是樣本平均值 $\overline{X}$

④顯著水準 α；危險域（Critical region）是

$$\overline{X} < \mu_0 - Z_{\alpha/2}\frac{\sigma}{\sqrt{n}} \quad 和 \quad \overline{X} > \mu_0 + Z_{\alpha/2}\frac{\sigma}{\sqrt{n}}$$

接受範圍是

$$\mu_0 - Z_{\alpha/2}\frac{\sigma}{\sqrt{n}} \leqslant \overline{X} \leqslant \mu_0 + Z_{\alpha/2}\frac{\sigma}{\sqrt{n}}$$

這也就是說如果 $Z = (\overline{X} - \mu) / \frac{\sigma}{\sqrt{n}}$ 大於 $Z_{\alpha/2}$ 或小於 $-Z_{\alpha/2}$，我們就否定 H_0，不然 H_0

就被接受。如果 σ^2 是未知數，s^2 就用來代替 σ^2 。

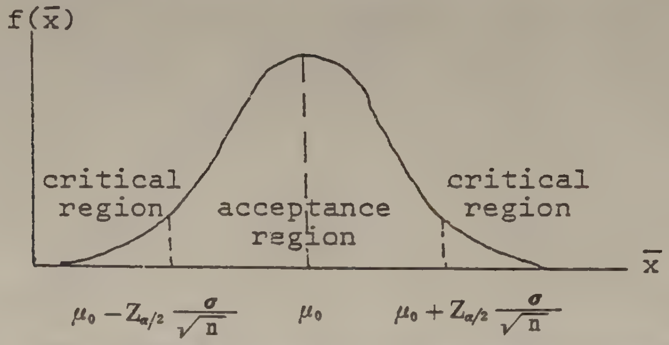

$f(\bar{x})$
critical region
acceptance region
critical region
$\bar{x}$
$\mu_0 - Z_{\alpha/2}\frac{\sigma}{\sqrt{n}}$
μ_0
$\mu_0 + Z_{\alpha/2}\frac{\sigma}{\sqrt{n}}$

圖 2.5　The acceptance region and critical region of normal distributed sample mean $\bar{x}$.

例 2.5　1969 調查中，七歲大的鰹魚（ Bonito ）的魚體長的次數如下：

Length cm X	Frequency f
66	3
69	7
70	7
71	8
72	10
73	3
74	3
75	1
77	1
	43

請檢定體長平均值是 72 cm，運用顯著水準 5 %，並計算平均值的 95 % c.i.

Solution:　$H_0 \quad \mu = 72 \qquad \alpha = .05$

$H_a \quad \mu \neq 72$

$$\bar{X} = \frac{\Sigma f X}{\Sigma f} = \frac{3052}{43} = 70.97$$

$$s^2 = \frac{\Sigma f X^2 - \frac{(\Sigma f X)^2}{n}}{n-1} = \frac{216832 - 216621.0233}{42}$$

$$= \frac{210.9767}{42} = 5.02$$

$$Z = \frac{\overline{X} - \mu_0}{\frac{s}{\sqrt{n}}} = \frac{70.97 - 72}{\sqrt{\frac{5.02}{43}}} = \frac{-1.03}{.3416} = -3.01$$

$$Z_{\alpha/2} = 1.96$$

$$Z < -Z_{\alpha/2}$$

we reject H_0 $\mu = 72$.

95 % c.i. for μ is

$$\overline{X} \pm 2\frac{s}{\sqrt{n}}$$

$$= 70.92 \pm 2\ (\ .3416\ )$$

$$= 70.92 \pm .6832$$

$$= (\ 70.23\ ,\ 71.6\ )$$

例 2.6　在一次海洋調查中，第 12 站的漁獲量包括 51 條 Dover sole ，其中 27 條是雄性， 24 條是雌性。檢定性比 1：1 的假設。

Solution：　Let p = population percentage of males.

q = population percentage of females.

H_0 :　$p = q = \frac{1}{2}$

H_a :　$p \doteqdot q$

$n = 51$

$\hat{p} = \frac{27}{51}$

under the H_0

$$\sigma^2_{\hat{p}} = \frac{p\,(\,1-p\,)}{n} = \frac{\frac{1}{2} \cdot \frac{1}{2}}{51} = \frac{1}{(\,51\,)(\,4\,)} = .0049$$

$$Z = \frac{\hat{p} - \frac{1}{2}}{\sigma_{\hat{p}}} = \frac{\frac{27}{51} - \frac{1}{2}}{\sqrt{.0049}} = .42$$

$$Z_{\alpha/2} = 1.96$$

since $Z < Z_{\alpha/2}$,　　we do not reject the H_0 .

b、小樣本統計檢定

假如樣本來自土堆形分配的母體，關於母體平均值的假設檢定，可以依照下列步驟:

如果母體變方（ σ^2 ）已知，Z 檢定法（ $Z = (\overline{X} - \mu) / \frac{\sigma}{\sqrt{n}}$ ）可用於樣本大的統計檢定，如果 σ^2 是未知數，樣本變方（ s^2 ）可用來代替 σ^2 ，那麼 $t = (\overline{X} - \mu) / \frac{\sigma}{\sqrt{n}}$ ，就不

是常態分配了，統計量 t 是 Student's t 分配，它的形狀隨 n 而變，當 n 很大時，t 就趨近常態分配，請注意 t 是 $\overline{X}$，s 和 n 的函數，同時 $s^2 = \frac{\Sigma(X-\overline{X})^2}{n-1}$。t 分配隨樣本大小（n）而不同。

對於任何 n，t 是 t 分配並有 n−1 d.f.。在表中之 t_α 值，符合於 $p(T > t_\alpha) = \alpha$，$\alpha = 0.1, 0.05, 0.025, 0.01, 0.005$。像常態分配一樣 t 分配是以零爲對稱的，這就是說 $p(T > t_\alpha) = p(T < -t_\alpha)$，t 檢定法與 Z 檢定法是一樣的，不同處是用 t 表來決定危險值（Critical value）而不用常態表。

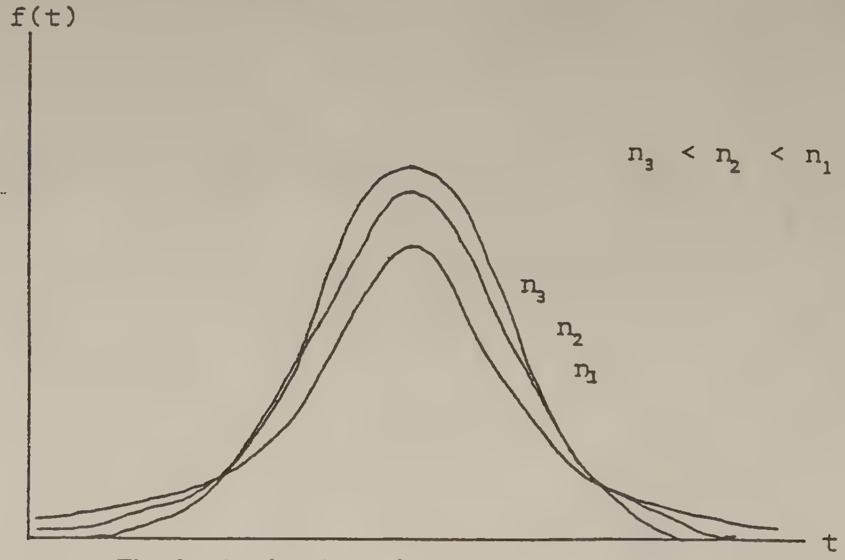


圖 2.6　The density functions of t statistics with different sample sizes, where $n_3 < n_2 < n_1$.

例 2.7　1973 Razor 蚌調查中，在低潮水的週末，樣本中有蚌數量爲 0，10.3，14.6，7.4，16.2，18.7，17.5 和 15.9，這些資料能證明平均值是 14 嗎？

Solution：　H_0：$\mu = 14$

H_1：$\mu \neq 14$

$n = 8$

$$\overline{X} = \frac{\Sigma X}{n} = \frac{100.6}{8} = 12.57$$

$$s^2 = \frac{\Sigma(X-\overline{X})^2}{n-1} = \frac{\Sigma X^2 - \frac{(\Sigma X)^2}{n}}{n-1} = \frac{1545.2 - 1265.045}{7} = \frac{280.155}{7}$$

$$= 40.02$$

$$t = \frac{\overline{X} - \mu_0}{\frac{s}{\sqrt{n}}} = \frac{12.57 - 14}{\sqrt{\frac{40.02}{8}}} = -.64$$

$$t_{.025,d.f.=7} = 2.365$$

$$|t| < 2.365$$

we don't reject the H_0 : $\mu = 14$.

c、α 和 β 的關係

顯著水準 α，其定義爲犯“型一誤差”的機率，而 β 是犯“型二誤差”的機率，α 和 β 的關係能從圖 2.7 看出；當 α 增加時 β 就減少，當 α 是保持常數，唯一方法去減少 β 就是增加樣本大小。$1-\beta$ 是在對立假設中確定了的參數價值後否定虛無假設的機率。$1-\beta$ 被稱爲測驗的檢力（Power of the test），從一連串的 μ 數值中（在對立假設下），一連串的 $1-\beta$ 可以計算出來。一個檢力曲線（Power curve）可以劃出來（圖 2.8）。

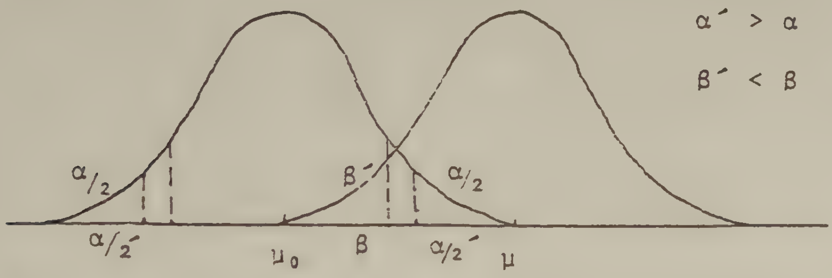


圖 2.7　The relationship between type Ⅰ error, α, and type Ⅱ error, β.

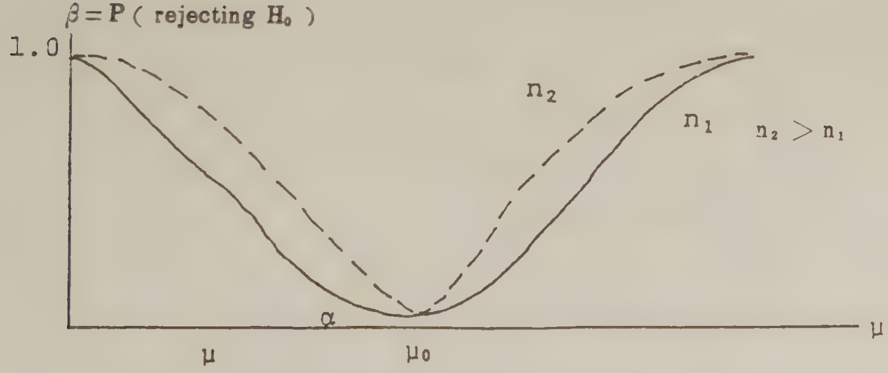


圖 2.8　The power curves of test with two sample sizes：$n_2 > n_1$.

$$P(\text{Rejecting } H_0) = P\{\overline{X} > \mu_0 + 2\frac{\sigma}{\sqrt{n}} \text{ or } \overline{X} < \mu_0 - 2\frac{\sigma}{\sqrt{n}} \mid \mu\}$$

$$= P\{ |X - \mu_0| > 2\frac{\sigma}{\sqrt{n}} \mid \mu\}$$

例 2.8　用例 2.5 的資料必須有多少觀察量（n = ?）才能測出與母體平均值之差是 1 cm，其概率是 90 %。

Solution：　H_0 ：　$\mu = 72$

H_a ：　$\mu = 71$ or 73

the rejection region is

$$\overline{X} < 72 - 1.96\sqrt{\frac{5.02}{n}} \text{ and } \overline{X} > 72 + 1.96\sqrt{\frac{5.02}{n}}$$

the acceptance region is

$$72 - 1.96\sqrt{\frac{5.02}{n}} < \overline{X} < 72 + 1.96\sqrt{\frac{5.02}{n}}$$

$$\beta = P(\text{accept the } H_0 \mid \mu = 71 \text{ or } 73) = 1 - .9 = .1$$

Because of the symmetry of the normal distribution. We only need to calculate sample size when one of the alternatives is true.

$$\beta = P(72 - 1.96\sqrt{\frac{5.02}{n}} < \overline{X} < 72 + 1.96\sqrt{\frac{5.02}{n}} \mid \mu = 73) = .1$$

$$P\left(\frac{72 - 1.96\sqrt{\frac{5.02}{n}} - 73}{\sqrt{\frac{5.02}{n}}} < \frac{\overline{X} - 73}{\sqrt{\frac{5.02}{n}}} < \frac{72 + 1.96\sqrt{\frac{5.02}{n}} - 73}{\sqrt{\frac{5.02}{n}}}\right) = .1$$

$$\beta = P\left(\frac{72 - 73 - 1.96\sqrt{\frac{5.02}{n}}}{\sqrt{\frac{5.02}{n}}} < Z < \frac{72 - 73 + 1.96\sqrt{\frac{5.02}{n}}}{\sqrt{\frac{5.02}{n}}}\right)$$

$$= P(Z_0(n) < Z < Z_1(n))$$

$n = 10$　　　$Z_0 = 3.37$　　　$Z_1 = .5486$

$$\beta = P(-3.37 < Z < .5486) = .5 + .2 = .70$$

Therefore we know n has to be greater than 10 and Z_0 can be taken as $-\infty$.

We need to solve the equation

$$P(-\infty < Z < Z_1(n)) = .1$$

The normal table indicates that

$$Z(n) = -1.28$$

$$\rightarrow \quad \frac{72-73+1.96\sqrt{\frac{5.02}{n}}}{\sqrt{\frac{5.02}{n}}} = -1.28$$

$$\rightarrow \quad 3.24\sqrt{\frac{5.02}{n}} = 1$$

$$\rightarrow \quad n = 53$$

Problems:

1. Referring to EX 1.3, how would you conduct a hypothesis testing at 5% level of significance? Write down the null hypothesis, alternative hypothesis, test statistic and the critical region. From the sample result, what is your conclusion? How large should the sample size be in order to detect a difference of .1 90% of the time?
2. A sample of 14 crabs were taken from Eureka area for tissue analysis. Their Ag contents are as follows: 7.9, 7.2, 12.2, 9.9, 10.5, 28.3, 15.5, 12.8, 20.3, 19.0, 18.1, 8.0, 2.1, 1.5. Calculate 95% c.i. for the average Ag in crab tissue.
3. A fisheries biologist believes that the population of trout in a particular lake should be held at the 10,000 level for optimum fishing and continued stability of the fishery. He takes samples periodically having first marked 500. If a sample of size 200 fish is taken, what should be his decision rule choosing between

   a. This population is 10,000

   and b. The population is above or below 10,000.

   Stating that b is true when in fact a is constitutes the more important type of error, the probability of which he would like to hold at .10

   1. If in a sample of 200 fish, 6 of them are marked fish. What will your conclusion be?
   2. If there are actually 8,000 fish in the lake, how often will you conclude that there are 10,000 fish in the lake?
4. From investigations off Japan, Wilke has shown that 90% of adult female seals are pregnant during the winter season. Of seven seals taken off Alaska one winter only two were pregnant. Is there reason to believe that either this is

not a random sample of North American fur seals or that the proportion of pregnancies differs from Asiatic seals?

5. The following are the petrale sole data in a sample taken from the boat ALEX PALADINI at San Francisco Bay, February 1, 1974.

Male	Female	
362	426	396
346	488	368
344	442	420
352	414	436
350	408	476
370	382	430
352	414	
348	410	
362	442	
344	390	
374	414	
350	418	
362	380	
336	410	
334	474	
350	426	
342	378	
342	380	
336	440	
360	366	
368	434	
354	410	

   a. Calculate the point estimates and 95% c.i. of the average length for the male and female.

   b. Calculate the 95% c.i. for the percentage of females in the catch by this boat.

6. During February 1968, the crab cruise had in the sample 30 legal male crabs out of 195 males from depths greater than 30 fm. Since the trawl net was used, it is assumed that there were few escapements. Therefore it is reasonable to use the sample data to estimate the population proportion of legal crab. Calculate 95% c.i. for the percentage of legal crabs from that depth.

三、迴歸分析（ Regression Analysis ）

如果有一組成對的資料（X_1 , Y_1 ），……，（X_n , Y_n ），我們欲知道兩個隨機變數（ X , Y ）的關係，他們的關係可能是互相依賴或者單方依賴，或者是兩者皆是。例如體重和身高的關係是互相依賴，但用身高去預測體重，則是說體重依賴於身高，然而有些情形只有單方依賴是研究的對象，例如：要預測明年釣魚執照的發給乃是靠著今年執照發給的多少，還有如產卵總群和加入魚群（ Spawning stock 和 Recuritment ）的關係。我們只可說適合的溫度促使好的加入魚群，而不能反說。研究相互依賴關係的是相關理論，研究單方依賴的是迴歸分析。

線性模式

想要從已知的X值去預測Y的平均值EY_x，我們必須先決定X和Y的關係，當EY_x是一個X的線性函數，即

$$EY_x = \alpha + \beta X \qquad (3.1.a)$$

或是 $$EY_x = \mu_y + \beta(X - \mu_x) \qquad (3.1.b)$$

α 是截距（ Intercept ）（請勿與顯著水準之 α 相混）

β 是斜率（迴歸係數）（請勿與型二誤差之 β 相混）

因此我們說X和Y有一個線性關係或者是Y是迴歸於X，同樣地X也可以迴歸於Y，那麼我們就有

$$EX_Y = \alpha_1 + \beta_1 Y \qquad (3.2.a)$$

或是 $$EX_Y = \mu_x + \beta_1(y - \mu_y) \qquad (3.2.b)$$

用（3．1）或（3．2）是看情形而決定，方法是一樣的，如果Y是迴歸於X，Y被稱爲因變數（ Dependent variable ），X被稱爲自變數（ Independent variable ）。

因爲普通X和Y的樣本是抽自兩變數的（ Bivariate ）母體，係數α和β都是未知數，須要估計。如何估計是本章的主題，最常用的方法是叫最小平方法（ Least squares method — LS ）。LS估計值$\hat{\alpha}$和$\hat{\beta}$如果符合下列條件則是α和β的最小變異和不偏差的估計：

a、對任何一個X，Y是常態分配，平均值是$\mu_{yx} = EY_x$和變異數（變方）σ_y^2。

b、變異數σ_y^2是常數，不隨X而變。

c、觀察值Y_i和Y_j，$i \neq j$都是獨立的，不互相依賴。（3．1）可以寫成

$$Y_x = \alpha + \beta X + e$$

Y_x是觀測值，e是誤差項，上述三個條件是說e是常態分配，其平均值是零和變異數是$\sigma_e^2 = \sigma_y^2$，e_i和e_j是獨立的（圖3.1）。

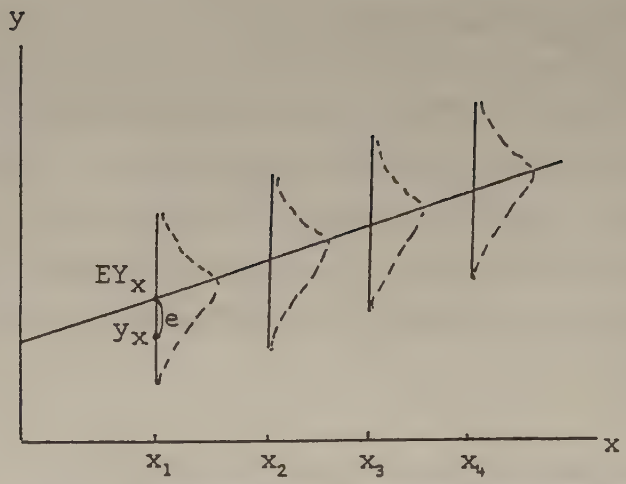


圖 3.1　A linear probabilistic model for fixed independent variable X .

3.1　**模式一：**獨立變數X是固定的。

對任何一組資料（X，Y），X值是可以控制的而不是隨機變數，對每一個X，一些觀測（Y′s）被記下來。例如X′s可能是五種魚網的網目大小（1.40″，1.45″，1.50″，1.55″和1.60″），假設沒有度量的誤差（Measurement error），每一頂魚網，拖網數次，漁獲量是Y′s。網目大小是可控制的，但是漁獲量是隨機變數，資料如下：

1.40″	1.45″	1.50″	1.55″	1.60″
y_{11}	y_{12}	y_{13}	y_{14}	y_{15}
y_{21}	y_{22}	y_{23}	y_{24}	y_{25}
⋮	⋮	⋮	⋮	⋮
$y_{n_1 1}$	$y_{n_2 2}$	$y_{n_3 3}$	$y_{n_4 4}$	$y_{n_5 5}$

3.2　**模式二：**

X和Y均爲常態分配，被抽樣的母體是兩變數的常態分配：

$$\begin{bmatrix} X \\ Y \end{bmatrix} \sim N\left(\begin{Bmatrix} \mu_x \\ \mu_y \end{Bmatrix},\ \begin{Bmatrix} \sigma^2 x & \rho\sigma_x\sigma_y \\ \rho\sigma_x\sigma_y & \sigma^2 y \end{Bmatrix}\right)$$

ρ是X和Y的相關係數，$\rho\sigma_x\sigma_y$是X，Y的變積（Covariance）。例如，一個成長的孩童的身高和體重是兩變數（Bivariate）的常態分配，兩個線性方程式將是如下：

$$EY_x = \mu_y + \rho\frac{\sigma_y}{\sigma_x}(x - \mu_x) \qquad (3.3)$$

with $\sigma_{yx}^2 = \sigma_y^2 (1-\rho)$ $\rho \frac{\sigma_y}{\sigma_x} = \beta$ in (3.1)

and $$EX_y = \mu_x + \rho \frac{\sigma_x}{\sigma_y} (y - \mu_y) \qquad (3.4)$$

with $\sigma_{xy}^2 = \sigma_x^2 (1-\rho)$ $\rho \frac{\sigma_x}{\sigma_y} = \beta_1$ in (3.2).

不論獨立變數的性質如何，適用（Fitting）線式模式的假定是一樣的，一般而言使用的方法是最小平方法（LS）。

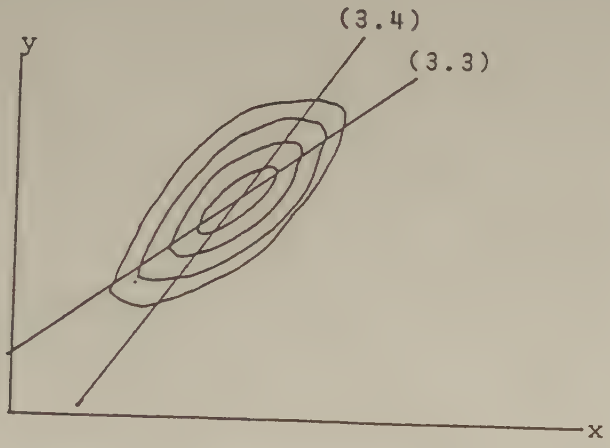


圖 3.2 Linear relationship of X and Y when X and Y are normal r.v.s.

3.3 用LS來估計 α 和 β

當 n 對觀測（X_1，Y_1），……（X_n，Y_n）用來選擇一個線性模式時，LS 估計值 $\hat{\alpha}$，$\hat{\beta}$ 是使觀測值 Y_x 和線上的數值 EY_x 之差的平方總和是最小值。使用 $\hat{\alpha}$ 和 $\hat{\beta}$，我們找出一條線最靠近 n 對觀測點，這些平方總和（Sum of squares；SS）可以寫成：

$$\begin{aligned} SS &= \Sigma (Y_x - EY_x)^2 \\ &= \Sigma \{ Y_x - (\alpha + \beta x) \}^2 = \Sigma e^2 \qquad (3.5) \end{aligned}$$

要使 SS 方程式（3.5）的值最小，我們須針對 α，β 取 SS 的微分：

$$\frac{\partial SS}{\partial \alpha} = 0 \qquad (3.6)$$

和 $$\frac{\partial SS}{\partial \beta} = 0 \qquad (3.7)$$

解聯立方程式（3.6）和（3.7），我們即得α和β的LS估計值：

$$\hat{\alpha}=\overline{Y}-\hat{\beta}\overline{X} \tag{3.8}$$

$$\hat{\beta}=\frac{\Sigma(X-\overline{X})(Y-\overline{Y})}{\Sigma(X-\overline{X})^2} \tag{3.9}$$

估計線性模式是

$$\hat{Y}_x=\hat{\alpha}+\hat{\beta}X \tag{3.10.a}$$

或 $$\hat{Y}_x=\overline{Y}+\hat{\beta}(X-\overline{X}) \tag{3.10.b}$$

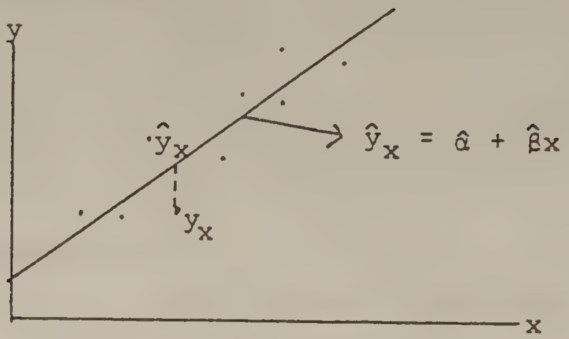


圖 3.3　The linear prediction equation.

共同變異數σ^2是由下列來估計

$$S_{yx}^2=\frac{\Sigma(Y-\hat{Y}_x)^2}{n-2} \tag{3.11}$$

根據誤差項（e）之常態分配的假定：其平均值是0，變異數是σ^2，我們能夠建立有關於母數α，β信賴區間和假設檢定和預測值EY_x。

迴歸係數β之符號說明X和Y之間的正、負和“零”關係。LS估計值$\hat{\beta}$是一個Y的線性函數，也是常態分配，其平均值是β，變異數是

$$\sigma_{\hat{\beta}}^2=\frac{\sigma^2}{\Sigma(X-\overline{X})^2}$$

$$\text{i.e.}\quad \hat{\beta}\sim N\left(\beta,\ \frac{\sigma^2}{\Sigma(X-\overline{X})^2}\right)$$

如果σ^2是未知數，$\sigma_{\hat{\beta}}^2$的估計為

$$s_{\hat{\beta}}^2=\frac{S_{yx}^2}{\Sigma(X-\overline{X})^2}\qquad \text{with } n-2 \text{ d.f.}$$

β的$1-\alpha$信賴區間

$$\hat{\beta}\pm t_{\alpha/2,\,n-2}\cdot s_{\hat{\beta}}$$

t 檢定法可以用來檢定虛無假設 $\beta=\beta_0$，針對對立假設 $\beta \neq \beta_0$ 。

where $$t=\frac{\beta-\beta_0}{s_{yx}\sqrt{\frac{1}{\Sigma(x-\overline{x})^2}}} \quad \text{with } n-2 \text{ d.f.}$$

針對一已知 X，Y 的預期值的估計如下：

$$\begin{aligned}\hat{y}_x &= \hat{\alpha}+\hat{\beta}x \\ &= \overline{y}+\hat{\beta}(x-\overline{x})\end{aligned}$$

因爲 $\overline{Y}$ 和 $\hat{\beta}$ 都是常態分配，Y_x 是 $\overline{Y}$ 和 $\hat{\beta}$ 的線性組合，$\hat{Y}_x$ 也將是常態分配，其值爲 EY_x，變方爲

$$\begin{aligned}\sigma^2_{\hat{y}_x} &= \sigma_{\overline{y}}^2+(x-\overline{x})^2\cdot\sigma^2_{\hat{\beta}} \\ &= \frac{\sigma^2}{n}+\frac{\sigma^2}{\Sigma(x-\overline{x})^2}\cdot(x-\overline{x})^2 \\ &= \sigma^2\left(\frac{1}{n}+\frac{(x-\overline{x})^2}{\Sigma(x-\overline{x})^2}\right) \qquad (3.12)\end{aligned}$$

or $$s^2_{\hat{y}_x}=s^2_{yx}\left(\frac{1}{n}+\frac{(x-\overline{x})^2}{\Sigma(x-\overline{x})^2}\right) \qquad (3.13)$$

EY_x 的 $1-\alpha$ 信賴區間是

$$\hat{y}_x \pm t_{\alpha/2,\,n-2}\sqrt{\left\{s^2_{yx}\left(\frac{1}{n}+\frac{(x-\overline{x})^2}{\Sigma(x-\overline{x})^2}\right)\right\}}\ .$$

從方程式（3.13）可看出，$\hat{Y}_x$ 的變異在 X 等於 $\overline{X}$ 時是最小，X 愈遠離 $\overline{X}$，$\sigma_{\hat{y}_x}^2$ 就愈大，如圖 3.4 所示。

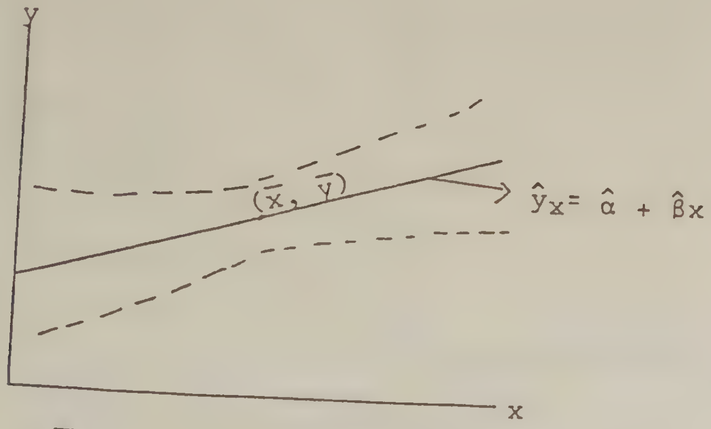

y
x
$(\overline{x}, \overline{y})$
$\hat{y}_x = \hat{\alpha} + \hat{\beta}x$

圖 3.4 The confidence band of EYx.

對 EY_x 的假設檢定是同樣的。

至於 α，自方程式（3.8）它的 LS 估計值的變方是

$$\sigma_{\hat{a}}^2 = \frac{\sigma^2}{n} + \frac{\sigma^2}{\Sigma(x-\bar{x})^2}\cdot\bar{x}^2$$

$$= \sigma^2\left(\frac{1}{n}+\frac{\bar{x}^2}{\Sigma(x-\bar{x})^2}\right)$$

樣本變方是

$$s_{\hat{a}}^2 = s_{yx}^2\left(\frac{1}{n}+\frac{\bar{x}^2}{\Sigma(x-\bar{x})^2}\right) \qquad (3.14)$$

$\hat{\alpha}$ 也是常態分配變數，其平均值是 α ，變方是

$\sigma_{\hat{a}}^2$ ，α 的 $1-\alpha$ 信賴區間是

$$\hat{\alpha}\pm t_{\alpha/2,n-2}\sqrt{s_{yx}^2\left(\frac{1}{n}+\frac{\bar{x}^2}{\Sigma(x-\bar{x})^2}\right)\}}$$

常常我們欲知資料是否通過原點，其虛無假設將是 $\alpha=0$ 。

例 3.1　下列是仔魚身長（mm）和年齡（時間）（小時）的一些簡化資料，假設成長在 15 週內是直線性之連續變數且成長率相同。

a 、在何極限內我們會 99 %的確定其生長率。

b 、推算 10 週大仔魚的平均身長。

	x_i (time)	y_i (length)	$(x_i-\bar{x})$	$y_i(x_i-\bar{x})$	$(x_i-\bar{x})^2$	$\hat{y}_i$	$(\hat{y}_i-y_i)^2$	y_i^2
	0	63	−5	−315	25	61.4	2.56	3969
	1	66	−4	−264	16	65.4	.36	4356
	2	68	−3	−204	9	69.4	1.96	4624
	3	73	−2	−146	4	73.4	.16	5329
	4	77	−1	− 77	1	77.4	.16	5929
	5	80	0	0	0	81.4	1.96	6400
	6	84	1	84	1	85.4	1.96	7056
	7	89	2	178	4	89.4	.16	7921
	8	96	3	288	9	93.4	6.76	9216
	9	99	4	396	16	97.4	2.56	9801
	10	100	5	500	25	101.4	1.96	10000
TOTAL	55	895	0	440	110		20.56	74601

Solution:　The time period (x_i) is a fixed value. The length (Y) is subject to error, i.e. Y is a random variable.

The LS estimates for β and α are

$$\hat{\beta}=\frac{\Sigma(x-\bar{x})(y-\bar{y})}{\Sigma(x-\bar{x})^2}=\frac{\Sigma(x-\bar{x})y}{\Sigma(x-\bar{x})^2}=\frac{440}{110}=4$$

and $\hat{\alpha}=\bar{y}-\hat{\beta}\bar{x}=\frac{895}{11}-4.5=81.4-20=61.4$

We have

$$\hat{y}_x=\hat{\alpha}+\hat{\beta}x=61.4+4x$$

The sample variance is

$$s_{yx}^2=\frac{\Sigma(y-\hat{y}_x)^2}{n-2}=\frac{20.56}{11-2}=2.28$$

a、The answer to this question is to construct the 99% c.i. for β. Since $1-\alpha = .99$, we have $\alpha=.01$

$$\hat{\beta}\pm t_{.005,9}\frac{s_{yx}}{\sqrt{\Sigma(x-\bar{x})^2}}$$

$$=4\pm 3.25\sqrt{\frac{2.28}{110}}$$

$$=4\pm .47=(3.53,\ 4.47)$$

b、Estimate the average length of a fingerling at week 10.

$$\hat{y}_{10}=61.4+4(10)=101.4$$

$$s_{\hat{y}_{10}}^2=s_{yx}^2\left(\frac{1}{n}+\frac{(x-\bar{x})^2}{\Sigma(x-\bar{x})^2}\right)$$

$$=2.28\left(\frac{1}{11}+\frac{(10-5)^2}{110}\right)$$

$$=2.28\left(\frac{1}{11}+\frac{25}{110}\right)=.7254$$

$$s_{\hat{y}_{10}}=.8517$$

95% c.i. for EY_{10} is

$$\hat{y}_{10}\pm t_{.025,9}\, s_{\hat{y}_{10}}$$

$$=101.4\pm 3.25(.8517)$$

$$=101.4\pm 2.768=(98.632,\ 104.168).$$

例 3.2　在一次加州鯡魚（Herring）調查中，獲得 4 歲鯡魚魚卵數量和身長的資料：

X length (mm)	Y number of eggs
163	14083
168	16985
168	16380
171	15135

172	13526
176	15052
193	25294
194	24309

a 、迴歸是否顯著？

b 、找出 4 歲鯡魚其魚身長爲 200 mm 之預期魚卵數量的 95 %信賴區間。

Solution： $n=8$

$$\Sigma x = 1405 \qquad \Sigma y = 140754$$

$$\Sigma x^2 = 247703 \qquad \Sigma y^2 = 2624423036$$

$$\Sigma xy = 25062246$$

$$\hat{\beta} = \frac{\Sigma xy - \frac{\Sigma x \Sigma y}{n}}{\Sigma x^2 - \frac{(\Sigma x)^2}{n}} = \frac{25062246 - \frac{(1405)(140754)}{8}}{247703 - \frac{(1405)^2}{8}} = 360.389$$

$$\hat{\alpha} = \bar{y} - \hat{\beta}\,\bar{x} = \frac{140754}{8} - 360.389 \cdot \frac{1405}{8} = 17594.25 - 63{,}293.318$$

$$= -45699.068$$

$$y = -45699.068 + 360.389 \cdot x$$

$$s_{yx}^2 = \frac{\Sigma(y - \hat{y}_x)^2}{n-2}$$

$$= \frac{\Sigma(y-\bar{y})^2 - \frac{\{\Sigma(x-\bar{x})(y-\bar{y})\}^2}{\Sigma(x-\bar{x})^2}}{n-2}$$

$$= \frac{\Sigma y^2 - \frac{(\Sigma y)^2}{n} - \frac{\{\Sigma xy - \frac{\Sigma x \Sigma y}{n}\}^2}{\Sigma x^2 - \frac{(\Sigma x)^2}{n}}}{n-2}$$

$$= \frac{147{,}961{,}971 - \frac{\{342324.75\}^2}{949.875}}{6}$$

$$= \frac{24{,}591{,}807}{6} = 4{,}098{,}634.5$$

a 、 $H_0 : \beta = 0$

$H_a : \beta \neq 0$

$$t = \frac{\hat{\beta} - 0}{s_{\hat{\beta}}} = \frac{360.389}{\sqrt{\left\{\frac{s_{yx}^2}{\Sigma(x-\bar{x})^2}\right\}}} = \frac{360.389}{\sqrt{\left\{\frac{4{,}098{,}634.5}{949.88}\right\}}} = \frac{360.389}{65.58} = 5.486$$

$t_{.025,6} = 2.44$

$t > t_{.025,6}$

We reject the H_0 and conclude that the regression is significant.

b、 $\hat{y}_{200} = -45699.068 + 360.389(200) = 26378.732$

$$s^2_{\hat{y}_{200}} = s^2_{yx}\left\{\frac{1}{8} + \frac{(200-\overline{x})^2}{\Sigma(x-\overline{x})^2}\right\}$$

$$= 4098634.5\left\{\frac{1}{8} + \frac{(200-175.625)^2}{949.88}\right\}$$

$$= 3075984.99$$

$s_{\hat{y}_{200}} = 1753.84$

95 % c.i. for EY_{200} is

$\hat{y}_{200} \pm t_{.025,6}\, s_{\hat{y}_{200}}$

$= 26378.732 \pm 2.44\,(1753.858)$

$= 26378.732 \pm 4279.39$

$= (21783.809\,,\ 30658.122)$.

Problem

1. In an experiment at Cultis Lake 3600 numbered tags were put out. The following table gives the number of recoveries by block of 600:

group (X)	recoveries (Y)
1	85
2	81
3	76
4	58
5	60
6	100

Find an equation of the form $EY = \overline{y} + \beta(x-\overline{x})$. Is β significantly different from 0 at the 5% level of significance.

2. The percentage of 1-year-old females and the conditional index of the shrimp indicating the relative average weight of the ocean shrimp from 1964-1973 are as follows:

Year	X(Conditional index)	Y(% of 1-year-old females)
1964	1.28	47
1965	.95	58
1966	1.05	37
1967	1.08	65
1968	1.13	55
1969	.93	48
1970	1.09	55
1971	.75	42
1972	.78	42
1973	1.22	65

Fit a straight line for the data. Test at 5% level that the regression is significant. Construct the 95% c.i. for the % of 1-year-old females when the conditional index is 1.

3. The C/E for barracuda at Coronados Islands, Mexico, and the average of the first six months temperature from 1943 to 1973 is as follows.

Year	x (average temperature of the first 6 months)	$e=y-\hat{y}$	y (C/E) 1000 lb.	$\hat{y}$
1948	14.8	.4827	.893	.41023
49	15.	.2229	.764	.5411
50	14.8	.0697	.48	.41029
51	15.4	-.3117	.491	.8027
52	15.1	.0265	.633	.6065
53	14.7	.0242	.369	.3448
54	15.4	-.2097	.593	.80273
55	15.	-.1751	.366	.5411
56	14.6	-.0824	.197	.2794
57	15.9	0	1.129	1.129
58	16.6	.013	1.6	1.587
59	17.1	.386	2.302	1.914
60	15.6	.5155	1.449	.9335
61	15.4	.019	.821	.802
62	14.8	.323	.733	.410
63	15.4	.2163	1.019	.8027
64	15.2	-.0749	.597	.6719
65	15.2	.1801	.852	.6719
66	15.7	.3851	1.384	.9989
67	15.0	.3009	.842	.5411
68	15.8	-.448	.616	1.064
69	15.3	-.12536	.623	.74834
70	15.3	-.1303	.607	.7373
71	14.5	-.10806	.106	.21406
72	15.3	-.72972	.0076	.73732
73	15.7	-.8509	.148	.9989

Fit a straight line for the data and construct 95% c.i. for the regression coefficient β.

四、抽樣計劃（ Sampling Planning ）—簡單隨機抽樣

在前幾章裏，我們討論到在資料收集之後，對母體作推論的一些基本的統計方法，如果我們屢次使用此一抽樣計劃，以這種方式收集的資料，其樣本多半能代表母體。一個理想的抽樣計劃是在最低成本下得到母體的不偏差的精確推算。抽樣方法有許多，一般說來，可以分成：有目的的選擇（ Purposive selection ）和機率抽樣（ Probability sampling ）。有目的的選擇是抽樣人員主觀地選擇抽樣單位，至於機率抽樣則是按照某種隨機的計劃抽樣。在這章裏，我們將討論一種基本的機率抽樣計劃。

雖然在有些情形下全盤調查（ Census ）是必須的，但是抽樣比起全盤調查，有它的長處：

1. 較便宜。
2. 如果觀測具損壞性，則必須抽樣。
3. 較快速。
4. 在實際上抽樣可能有較精確的結果。因爲可僱用高素質的人員，給予精嚴的訓練。

在抽樣調查計劃中，一般程序可以略述如下：

1. 說明調查之目的。
2. 要抽樣的母體定義。
3. 決定要收集的資料。
4. 選擇收集資料方法，如郵寄或訪問。
5. 抽樣單位之選擇。
6. 如何抽樣。
7. 實地工作的組織。
8. 資料分析和摘要。
9. 對將來調查之資料貢獻。

雖然抽樣理論在某些步驟－2 ，3 ，4 和 7 不佔重要角色。但是好的抽樣有賴於各階段的良好工作，某一階段的處理不善，卽使其它方面都盡善盡美，都將不利於整個調查。抽樣理論是用來式化（ Formulate ）一個抽樣程序，以便在最低成本下，得到精確且不偏差之母數推算。因此，當比較兩個同樣都可供應精確的母數推算的抽樣計劃時，成本低的一個應認爲是較佳者。一般而言，抽樣成本是與樣本大小成正比。因此一個需要少量的樣本而能達到預計的精確推算的抽樣計劃是爲較佳者。

簡單隨機抽樣（ Simple Random Sampling ，SRS ）是指在一個抽樣計劃中，母體的

每一個單位都有同樣被抽取的可能性。在大多數的抽樣調查中，觀測單位不退還母體，這叫作不退還抽樣（ Sampling without replacement ）。如果母體是無限的，不退還抽樣和退還抽樣無大區別，但對有限母體，不退還抽樣是須特別留意的。

如果在母體中，有N個單元。樣本大小是n，根據組合定律，有C_n^N種可能的樣本。在SRS下，每一樣本被抽取的機會相同。所以觀察任何一樣本的機率是

$$\frac{1}{C_n^N}=\frac{1}{\frac{N!}{n!(N-n)!}} \qquad (4.1)$$

如果我們考慮每次抽一單位，則每一樣本單位被抽取的機率是$\frac{1}{N}$，剩下在母體裏的樣本單位被抽的機率是$\frac{1}{N-1}$，如此一直到n單位被抽，因此任一樣本的被抽機率是：

$$n!\,\frac{1}{N}\cdot\frac{1}{N-1}\cdots\cdots\frac{1}{N-n+1}=\frac{1}{\frac{N!}{n!(N-n)!}} \qquad (4.2)$$

n！是n個抽樣單位的排列，因爲每一單元的位置不關緊要。例如一個母體包括三個單元A、B和C，樣本的大小是2，被抽而不退還，可能的樣本是AB，BC和AC，所以有三個結果。如果使用（4.1）式，N=3，n=2，則抽到一特別樣本AB的機率是：

$$\frac{1}{C_2^3}=\frac{1}{\frac{3!}{2!\,1!}}=\frac{1}{3}$$

4.1　推算值的特性

母體平均值和母體總和，是將推算的參數，例如，漁獲量平均值是母體平均值，Biomass是母體總和，N是拖網總數，如果採用SRS，樣本平均值是母體平均值的不偏差估計，如果我們給予上例A，B，C三個數值1，2，3，母體平均值$\mu=\frac{1+2+3}{3}=2$，所有可能樣本，其大小爲2，可列如下：

樣　本 （ samples ）	觀測量 （ observations ）	樣本平均值 （ sample mean $\bar{y}$ ）
AB	1，2	1.5
AC	1，3	2
BC	2，3	2.5

μ，樣本平均值（$\overline{Y}$）的平均值，是

$$\frac{\Sigma\bar{y}}{C_n^N}=\frac{1.5+2+2.5}{3}=2$$

所以 $\mu_{\bar{y}} = \mu_y = 2$

來自有限母體的 $\bar{y}$ 的變方定義爲

$$\sigma_{\bar{y}}^2 = \frac{\sigma^2}{n} \, \frac{N-n}{N} \qquad (4.3)$$

σ^2 是 y 的變方 $= \dfrac{\Sigma(y-\mu_y)^2}{N-1}$

$\dfrac{N-n}{N}$ 稱爲有限母體修正因數（ Finite population correction ， fpc ），如果比率 $\dfrac{n}{N}$ 少於 5％， fpc 就不用了，因此，如果對母體而言，樣本大小是相對的很小，則一個有限母體可以視爲無限母體。

如果 σ^2 是未知數，樣本變方 s^2 是 σ^2 的不偏差推算。

$$s^2 = \frac{\Sigma(y-\bar{y})}{n-1}$$

$\bar{y}$ 的樣本標準誤差是

$$s_{\bar{y}} = \frac{s}{\sqrt{n}} \sqrt{\left(\frac{N-n}{N}\right)}$$

4.2 樣本大小的決定：

$\bar{y}$ 的標準誤差， $s_{\bar{y}}$ ，是度量 $\bar{y}$ 的精確度的一種方法。它受幾個因素的影響：y 的標準差 s ，樣本的大小 n ，和抽樣比率 $\dfrac{n}{N}$。 s 的變異是不能控制的，但是增加樣本大小 n ，可以增加 $\bar{y}$ 的精確度。當使用區間估計母體平均值時，特定的區間長度即決定樣本的大小，μ 的 $1-\alpha$ 信賴區間是

$$\bar{y} \pm Z_{\alpha/2} \frac{s}{\sqrt{n}} \sqrt{\left(\frac{N-n}{N}\right)}$$

信賴區間的一半濶度

$$d = Z_{\alpha/2} \frac{s}{\sqrt{n}} \sqrt{\left(\frac{N-n}{N}\right)} \qquad (4.4)$$

因此

$$n = \frac{\left(\dfrac{Z_{\alpha/2}\, s}{d}\right)^2}{1 + \left(\dfrac{Z_{\alpha/2}\, s}{d}\right)^2 \dfrac{1}{N}} \qquad (4.5)$$

當 $\dfrac{n}{N}$ 小於 5％，（4.5）可寫作

$$n = \left(\frac{Z_{\alpha/2}\, s}{d}\right)^2 \qquad (4.6)$$

因此如果參數的區間估計是研究的對象，則樣本大小可以由方程式（4.5）或（4.6

）來決定。統計學家須知多大的推算誤差（d)是生物學家能接納的，區間推算能包括母體平均值的機率和資料的波動性（s^2），然後他們（統計學家）才能計算出樣本的大小。

例4.1　生物學家欲推算A湖的魚體長。大約有1000條魚在湖中，從以前的調查資料中變方是 $s^2=1.5$。運用SRS，應該抽取多少魚來推算母體平均值在0.5 mm之內，只有1/20的機會是不準的。

Solution：　$N=1000$　　$d=0.5$

$s^2=1.5$　　$Z_{\alpha/2}=2$

Using equation（4.5）, we have

$$n=\frac{\frac{(4)\cdot(1.5)}{.25}}{1+\frac{(4)(1.5)}{.25}\ \frac{1}{1000}}=\frac{24}{1.024}=23.4$$

a sample size of 24 is needed.

另一種度量 $\bar{y}$ 的精確度的公式是變異係數（Coefficient of variation，CV）。$\bar{y}$ 的CV是定義爲 $\bar{y}$ 的標準誤差和它的平均值 μ 的比例

$$CV(\bar{y})=\frac{\sigma_{\bar{y}}}{\mu} \qquad (4.7)$$

如 $\sigma_{\bar{y}}$ 和 μ 是未知數，$s_{\bar{y}}$ 和 $\bar{y}$ 可用作代替

$$CV(\bar{y})=\frac{s_{\bar{y}}}{y} \qquad (4.8)$$

因爲常常生物參數平均值大的隨機變數的變異大，小的則變異小。而通常CV是一百分比，所以使用比較方便。CV也能用來決定樣本大小，對一種特殊試驗，CV通常是在某一範圍之限度內（Range），如果CV超出了正常限度，研究人員應開始懷疑是否計算錯誤或者特殊情形發生，而對試驗的正確性起了懷疑。我們必須知道沒有 $s_{\bar{y}}$ 和 $\bar{y}$ 的數值而用CV可能會造成誤解。

4.3　母體總和的推算：

母體總和，T_y，通常是用 $\hat{T}=N\bar{y}$ 來推算的。$\hat{T}$ 的樣本變方是

$$s_{\hat{T}}^2=N^2 s_{\bar{y}}^2=N^2\,\frac{s^2}{n}\,\frac{N-n}{N}=\frac{s^2}{n}\,N(N-n)$$

T的 $1-\alpha$ 信賴區間是

$$\hat{T}\pm t_{\alpha/2,\,n-1}\ s\sqrt{\left\{\frac{N(N-n)}{n}\right\}} \qquad (4.9)$$

Problem

1. In a population with $N = 6$, the value of y_i are 8, 3, 1, 11, 4 and 7. Calculate the sample mean $\overline{y}$ for all possible simple random samples of size 2. Verify that $\overline{y}$ is an unbiased estimate of μ_y.

2. From a previous survey the sample standard deviation of Ag in N.C. crab tissue is 7.35. In the future analysis how many crabs need to be taken in order to estimate the mean Ag content within 5 apart from a chance of 1 out of 20?

3. The 1973 razor clam survey at South Clam Beach, Ca. had the data for four strata as follows:

Tide Series		Stratum No.	Total Number of Diggers (N_h)	Standard Deviation (s_h)	Average Catch/Digger ($\overline{y}_h$)
-.9 &	Wkday	1	240	6.6	16.8
above	Wkends	2	152	5.75	16.0
-1.0 &	Wkday	3	627	7.12	12.5
below	Wkends	4	800	6.38	13.96

In order to estimate the total catch at the South Beach in 1974 within 1000 clams, how large a sample size should we take? How would you allocate the sample among the strata?

五、變方分析（The Analysis of Variance）

比較兩個母體平均值時，我們用t檢定來檢查兩個樣本平均值之不同。推而廣之；要測出k個母體平均值之不同，就須用F檢定，即F檢定統計值。一般檢定k個母體平均值相等的虛無假設的方法是檢查k個樣本平均值，並將變方分解成兩部份（在最簡單的情形下），一部份是樣本平均值間的變方，另一部份是樣本裏的變方，後者亦稱爲誤差項（Error term）。在虛無假設下，樣本間變方和樣本裏變方的比例應符合F分配，所以是一個F統計值。數目大的F值將導致否定虛無假設。這種變方之分解就叫做變方分析。

5.1 F統計值

如果兩個樣本之大小分別爲n_1和n_2，獨立來自兩個常態分配。其變方爲σ_1^2和σ_2^2，則F統計值被定義爲

$$F_{\nu_1 \nu_2} = \frac{\frac{s_1^2}{\sigma_1^2}}{\frac{s_2^2}{\sigma_2^2}} \qquad (5.1)$$

其自由度是ν_1和ν_2

s_i^2是來自第i個母體的樣本變方

$$\nu_i = n_i - 1 \qquad \text{for} \qquad i = 1, 2 \quad 。$$

注意每一F統計值有兩個自由度，第一個自由度是聯於分子的樣本變方，第二個是分母的樣本變方的自由度，F統計值用處之一是檢定兩個變方相等的虛無假設，但是F統計值在統計問題上更重要之功用是在變方分析。

5.2 完全隨機設計（Completely randomized design，crd）

完全隨機設計是最簡單的一種情形。通常研究人員欲知曉某一因素（Factor）對他所研究的資料的影響，此因素程度之不同被稱爲處理（Treatment）。每一處理決定一母體。自每一母體中隨機抽一樣本，然後再比較樣本平均值。例如，生物學家可能對魚自不同網目之逃出量感興趣。換言之，生物學家所欲知道的是網目大小的影響。因此我們說這個因素是網目大小，不同網目大小是處理方法。用每一網目隨意拖網所得之量度（Measurements）（魚獲量，或1歲仔魚之百分比等等），就是即將分析的資料。用於變方分析之F檢定的假設有：

1. 樣本是從k個母體隨機抽取的。

2. k 個母體均是常態分配。

3. k 個母體變方相同。

在這些假設中，最重要的是隨機抽樣。非常態分配會導致比實際指定較大的顯著水準。k 個母體之變方不相等時，可以由相等的樣本大小來彌補。總之，稍微與假設不符將不致造成 F 檢定的嚴重誤差（ Error ）。

一個變方分析之程序結構可用下列的例子說明：假如有 k 個處理方法（或 k 個母體），我們要檢定 k 個母體平均值相等的虛無假設，於是我們有

H_0 ： $\mu_1 = \mu_2 = \cdots\cdots = \mu_k$

H_A ： 至少有兩個 μ 是不相等的。

隨機抽取 k 個樣本大小爲 n_j 的樣本， $j = 1, \cdots\cdots, k$ 。資料如下：

處理方法（ Treatment ）

$$\begin{array}{ccccccc} T_1 & T_2 & \cdots\cdots & T_j & \cdots\cdots & T_k & \\ y_{11} & y_{12} & & y_{1j} & & y_{1k} & \\ y_{21} & y_{22} & & y_{2j} & & y_{2k} & \\ \vdots & \vdots & & \vdots & & \vdots & \\ y_{n_1 1} & y_{n_2 2} & \cdots\cdots & y_{n_j j} & \cdots\cdots & y_{n_k k} & \\ \hline \bar{y}_1 & \bar{y}_2 & & \bar{y}_j & & \bar{y}_k & , \bar{\bar{y}} \end{array}$$

$\bar{y}_j$ 是取自第 j 母體的樣本平均值

$\bar{\bar{y}} = \dfrac{\Sigma\Sigma y_{ij}}{\sum\limits_{j=1} n_j}$ 是總平均值。

所有基於總平均值量度（ Measurements ）的變量（ Variation ）可以用平方總和來表示（ Total sum of squares ， SST ）。

$$SST = \sum_{j=1}^{k} \sum_{i=1}^{n_j} (y_{ij} - \bar{\bar{y}})^2 \qquad (5.2)$$

SST 可分成兩個平方和：

$$\underset{SST}{\sum_{j=1}^{k} \sum_{i=1}^{n_j} (y_{ij} - \bar{\bar{y}})^2}$$

(5.3)

$$= \underbrace{\sum_{j=1}^{k}\sum_{i=1}^{n_j}(y_{ij}-\bar{y}_j)^2}_{SSE} + \underbrace{\sum_{j=1}^{k} n_j(\bar{y}_j-\bar{\mathbf{y}})^2}_{SSTr}$$

在公式(5.3)的右邊第一項是代表在每一樣本裏的變量，被稱爲誤差平方和（Error sum of square，SSE）。根據 k 個母體變方相等之假設，SSE 可用來計算聯合（Pooled）樣本變方，此乃爲公有變方（Common variance，σ^2）的不偏推算（Unbiased estimate）。第二項代表樣本間的變方，被稱爲處理之平方總和（Treatment sum of squares，SSTr）。SST 包括量度（Measurement）之間的變量和 k 個母體平均值的變量。檢查 k 個母體平均值之不同的一般方法是比較 SSTr 和 SSE，如果 SSTr 大於 SSE，其結論是 k 個母體之平均值不全相等。變方分析之程序如下：

首先，須知平方和的自由度，以便計算 F 統計值，平方和 SSE 和 SSTr 之自由度各爲 $\sum_{j=1}^{k}(n_j-1)$ 和 $k-1$。當我們計算樣本變方時，先定義均方誤差（Mean square error，MSE）爲平方和除以它的自由度。因此變方分析表（Analysis of variance table，ANOVA）是：

表 5.1　完全隨機設計之 ANOVA

變量來源 (Source of Variation)	平方和 (Sum of Squares)	自由度 (Degree of Freedom)	均方誤差 (Mean Square Error)	預期值 (Expectation)
Among Samples	$\sum_{j=1}^{k} n_j(\bar{y}_j-\bar{\mathbf{y}})^2$	$k-1$	$MSETr=\frac{SSTr}{d.f.}$	$\sigma^2+n^*\sigma_\mu^2$
Within Samples	$\sum_{j=1}^{k}\sum_{i=1}^{n_j}(y_{ij}-\bar{y}_j)^2$	$\sum_{j=1}^{k}(n_j-1)$	$MSEE=\frac{SSE}{d.f.}$	σ^2

＊n 均相等：　$n_j=n$

在 k 個母體平均值相等之虛無假設下，$\sigma_\mu^2=0$。MSETr 和 MSEE 之比例符合 F 分配，連同其自由度應爲

$$F_{\nu_1,\nu_2}=\frac{MSETr}{MSEE}=\frac{\sum_{j=1}^{k} n_j(\bar{y}_j-\bar{\mathbf{y}})^2/(k-1)}{\sum_{j=1}^{k}\sum_{i=1}^{n_j}(y_{ij}-\bar{y}_i)^2/\sum_{j=1}^{k}(n_j-1)}$$

自由度爲：

$$\nu_1 = k - 1$$

$$\nu_2 = \sum_{j=1}^{k} (n_j - 1)$$

當計算出之 F 值太大時，虛無假設即被否定。任何統計書籍均有 F 統計值的危險值（ Critical values ）的例表。

欲計算 SS，我們有下列便捷的方法。

表 5.2　完全隨機設計之ANOVA計算程序

Type of Total	Total of Squares per Observation	
grand	$(\Sigma\Sigma y_{ij})^2 / \sum_{j=1}^{k} n_j$	（Ⅰ）
treatment	$\sum_{j=1}^{k} (\sum_{i}^{n_j} y_{ij})^2 / n_j$	（Ⅱ）
observation	$\sum_{j=1}^{k} \sum_{i=1}^{n_j} y_{ij}^2$	（Ⅲ）

ANOVA Table

Source of Variation	Sum of Squares	Degree of Freedom	MS	F
Among Samples	（Ⅱ）−（Ⅰ）	$k - 1$		
Within Samples	（Ⅲ）−（Ⅱ）	$\Sigma n_j - k$		
TOTAL	（Ⅲ）−（Ⅰ）	$\Sigma n_j - 1$		

例 5.1　下列數量代表在產卵地區王鮭（ King salmon ）自標識放流到回收的時間（以星期計算）三個年齡類別是否有顯著的區別？

Solution：　H_0 ：　$\sigma_\mu^2 = 0$ （ $\mu_1 = \mu_2 = \mu_3$ ）

H_a ：　$\sigma_\mu^2 \neq 0$ （ not all μ_i's are equal ）

Samples from

	Population 1 (age 3)	Population 2 (age 4)	Population 3 (age 5)	
	3	4	3	
	2	9	1	
	6	5	2	
	3	6		
	1	2		
		3		
		8		
		4		
		7		
		1		
		5		
		6		
$\sum_i y_{ij}$:	15	60	6	$\Sigma\Sigma y_{ij} = 81$
n_j :	5	12	3	$\Sigma n_j = 20$
$\bar{y}_j$:	3	5	2	$\bar{y} = 4.05$

$$(\mathrm{I}) = \frac{(\Sigma\Sigma y_{ij})^2}{\Sigma n_j} = \frac{81^2}{20} = 328.05$$

$$(\mathrm{II}) = \sum_{j=1}^{k} \frac{\left(\sum_{i=1}^{n} y_{ij}\right)^2}{n_j} = \frac{15^2}{5} + \frac{60^2}{12} + \frac{6^2}{3} = 357$$

$$(\mathrm{III}) = \sum_{j=1}^{k} \sum_{i=1}^{n_j} y_{ij}^2$$

$$= 3^2 + 2^2 + \cdots\cdots + 1^2 + 4^2 + 9^2 + \cdots\cdots + 6^2 + 3^2 + 1^2 + 2^2$$

$$= 435$$

ANOVA Table

Source of Variation	SS	d.f.	MSE	F
Among Samples	28.95	2	14.475	3.1548
Within Samples	78	17	4.588	
TOTAL	106.95	19		

From the F table $F_{2,17,.05} = 3.59$

Since $3.15 < 3.59$ the hypothesis is not rejected at the 5% level of significance.

均方誤差（MSEE）是用來推算共同變方 σ^2，所以也用來計算母體（Population）平均值或兩個母體平均值之差的信賴區間。

μ_i 之 $1-\alpha$ 的信賴區間是

$$\bar{y}_i \pm t_{\alpha/2} \frac{s}{\sqrt{n_i}} \qquad (5.4)$$

$\mu_i - \mu_j$ 之 $1-\alpha$ 的信賴區間是：

$$(\bar{y}_i - \bar{y}_j) \pm t_{\alpha/2}\, s \sqrt{\left(\frac{1}{n_i} + \frac{1}{n_j}\right)} \qquad (5.5)$$

where

$$s = \sqrt{MSEE} = \sqrt{\frac{SSE}{\Sigma(n_i - 1)}}$$

其自由度 $= \Sigma(n_i - 1)$

在例 5.1 中求年齡 3 週和 4 週之平均時間差別的 95 %信賴區間。

運用（5.5）我們可得

$$(3-5) \pm t_{.025\,;\,17} \left\{4.588\left(\frac{1}{5} + \frac{1}{12}\right)\right\}^{\frac{1}{2}}$$

$$= -2 \pm (2.11)(1.14)$$

$$= (-4.4054\,,\ .4054)$$

例 5.2　比較五種網目所捕獲每磅之海蝦數，1968 年六月～七月 Eureka 商業漁船調查得到下列資料。以 5 %之顯著水準來檢定網目大小對漁獲量無影響的虛無假設。

Solution：

Mesh Sizes	1.31″	1.32″	1.33″	1.34″	1.4″	1.5″	
	106	97	100	100	107	97	
	121	102	94	94	112	112	
	108	101	115	92	94	104	
	100	105	122	106	100	96	
	98	96	95	109	119		
		89	99	100	101		
		91		107			
		98					
		102					
		88					
		83					
		88					
$\sum_i y_{ij}$:	533	1140	625	708	633	409	$\Sigma\Sigma y_{ij} = 4048$

n_j :	5	12	6	7	6	4	$\Sigma n_j = 40$
y_j :	106.6	95	104.17	101.14	105.5	102.25	$\bar{\bar{y}} = 101.2$

$$(\mathrm{I}) = \frac{(\Sigma\Sigma y_{ij})^2}{\Sigma n_j} = \frac{4048^2}{40} = 409657.6$$

$$(\mathrm{II}) = \sum_{j=1}^{k} \frac{(\sum_{i}^{n_j} y_{ij})^2}{n_j} = \frac{533^2}{5} + \frac{1140^2}{12} + \cdots\cdots + \frac{429^2}{4} = 410432.85$$

$$(\mathrm{III}) = \sum_{j=1}^{k} \sum_{i=1}^{n_j} y_{ij}^2 = 106^2 + 121^2 + \cdots\cdots + 104^2 + 96^2 = 412800$$

ANOVA Table

Source of Variation	SS	d.f.	MSE	F
Among Samples	775.25	5	155.05	2.227
Within Samples	2367.15	34	69.622	
TOTAL	3142.4	39		

$F_{5,34} = 2.5$

since $F < F_{5,34}$, the hypothesis is not rejected at 5% level.

5.3 隨機區集設計（Randomized block design, rbd）

隨機區集設計（rbd）是本章中將介紹的第二種設計。rbd 和 crd 不同處有如成對之 t 檢定和普通的 t 檢定。當用到 rbd 時，實驗單位（Experimental units）都將分組，如此在一組內（Within block）的變方將小於組間的變方，然後處理方法隨機地分配到每一組內的各個單位。

處理方法（Treatment）

		T_1	T_2	………	T_j	………	T_k	
組別（Block）	B_1	y_{11}	y_{12}		y_{1j}		y_{1k}	$\bar{y}_1.$
	B_2	y_{21}	y_{22}		y_{2j}		y_{2k}	$\bar{y}_2.$
	⋮	⋮	⋮		⋮		⋮	⋮
	B_i	y_{i1}	y_{i2}		y_{ij}		y_{ik}	$\bar{y}_i$

⋮	⋮	⋮	⋮	⋮	⋮
B_L	y_{L1}	y_{L2}	y_{Lj}	y_{Lk}	$\bar{y}_{L\cdot}$
	$\bar{y}_{\cdot 1}$	$\bar{y}_{\cdot 2}$	$\bar{y}_{\cdot j}$	$\bar{y}_{\cdot k}$	$\bar{\bar{y}}$

平方總和（SS）可以分成三個平方和：

$$\underset{SST}{\sum_{j=1}^{k}\sum_{i=1}^{L}(y_{ij}-\bar{\bar{y}})^2} \qquad (5.6)$$

$$=\underset{SSTr}{\sum_{j=1}^{k}L(\bar{y}_{\cdot j}-\bar{\bar{y}})^2}+\underset{SSB}{\sum_{i=1}^{L}k(\bar{y}_{i\cdot}-\bar{\bar{y}})^2}+\underset{SSE}{\sum_{i}^{k}\sum_{j}^{L}(y_{ij}-\bar{y}_{\cdot j}-\bar{y}_{i\cdot}+\bar{\bar{y}})^2}$$

SSB 是組平方和，其它的平方和在前已下定義了。

比較公式（5.6）和公式（5.3）可以看出，在（5.3）中的誤差項（ Error term ）是再加分解成兩個平方和。因此如果有組影響（ Block effect ），在 rbd 下的誤差項會比 crd 的誤差項要小。

rbd 的 ANOVA 表是列在表 5.3 內：

表 5.3　ANOVA　for rbd

變量來源 (Source of Variation)	平方和 (Sum of Squares)	自由度 (Degree of Freedom)	均方誤差 (Mean Square Error)	預期值 (Expectation)
treatment	$\sum_{j=1}^{k}L(y_{\cdot j}-\bar{\bar{y}})^2$	$k-1$	$MSETr=\frac{SSTr}{d.f.}$	$\sigma^2+L\sigma_{\mu_T}^2$
block	$\sum_{i=1}^{L}k(y_{i\cdot}-\bar{\bar{y}})^2$	$L-1$	$MSEB=\frac{SSB}{d.f.}$	$\sigma^2+k\sigma_{\mu_\beta}^2$
error	$\sum\sum(y_{ij}-\bar{y}_{\cdot j}-\bar{y}_{i\cdot}+\bar{\bar{y}})^2$	$(k-1)(L-1)$	$MSEE=\frac{SSE}{d.f.}$	σ^2
TOTAL	$\sum\sum(y_{ij}-\bar{\bar{y}})^2$	$kL-1$		

在虛無假設 H_0：$\mu_1=\mu_2=\cdots\cdots=\mu_k$ 或 $\sigma_{\mu_T}^2=0$ 之下，$\frac{MSETr}{MSEE}$ 符合 F 分配，並用來檢定 H_0，$\frac{MSEB}{MSEE}$ 的比率可用來檢定組影響（ Block effect ），即檢定 H_0，$\sigma_{\mu_\beta}^2=0$。

5.4　表給予所有SS便捷的計算公式

表 5.4

Computing Procedure of Analysis of Variance for rbd

Type of Total	Total of Squares per Observation	
grand	$(\Sigma\Sigma y_{ij})^2 / kL$	(Ⅰ)
treatment	$\sum_{j=1}^{k}(\sum_{i=1}^{L} y_{ij})^2 / L$	(Ⅱ)
block	$\sum_{i=1}^{L}(\sum_{j=1}^{k} y_{ij})^2 / k$	(Ⅲ)
observation	$\sum_{j=1}^{k}\sum_{i=1}^{L} y_{ij}^2$	(Ⅳ)

ANOVA 表

Source of Variation	Sum of Squares	Degree of Freedom	MS	F
treatment	(Ⅱ)−(Ⅰ)	$k-1$		
block	(Ⅲ)−(Ⅰ)	$L-1$		
error	(Ⅳ)−(Ⅱ)−(Ⅲ)+(Ⅰ)	$(k-1)(L-1)$		
TOTAL	(Ⅳ)−(Ⅰ)	$kL-1$		

例 5.3　下列資料是每一百磅飼料，豬增加的體重。自五窩中，每窩抽取體重相似的三隻。三種飼料（對體重增加）是否有顯著的不同？

Solution：

Litter	Feed 1	Feed 2	Feed 3	$\sum_{j=1}^{3} y_{ij}$	$\bar{y}_{i\cdot}$
1	15	22	25	62	20.67
2	21	23	24	68	22.67
3	22	31	25	68	22.67
4	17	20	23	60	20
5	17	22	26	65	21.67
$\sum_{i=1}^{5} y_{ij}$:	92	108	123		$\Sigma\Sigma y_{ij} = 323$
$\bar{y}_{\cdot j}$:	18.4	21.6	24.6		$\bar{y} = 21.53$

H_0 : $\sigma^2_{\mu_T} = 0$ or $\mu_1 = \mu_2 = \mu_3$

$$(\text{I}) = \frac{(\Sigma\Sigma y_{ij})^2}{k\,L} = \frac{323^2}{3 \times 5} = \frac{104329}{15} = 6955.267$$

$$(\text{II}) = \sum_{j=1}^{k} \frac{(\sum_{i=1}^{L} y_{ij})^2}{L} = (92^2 + 108^2 + 123^2)/5 = 7051.4$$

$$(\text{III}) = \sum_{i=1}^{L} \frac{(\sum_{j=1}^{k} y_{ij})^2}{k} = (62^2 + 68^2 + 68^2 + 60^2 + 65^2)/3 = 6972.333$$

$$(\text{IV}) = \Sigma\Sigma y^2 = 15^2 + 21^2 + \cdots\cdots + 23^2 + 26^2 = 7097$$

ANOVA Table

Source of Variation	SS	d.f.	MSE	F
treatment	96.133	2	48.0665	13.476
block	17.066	4	4.2665	1.196
error	28.534	8	3.56675	
TOTAL	141.733	14		

$F_{2,8,0.05} = 4.46$

since $13.476 > 4.46$, the H_0 is rejected at the 5% level. As to the block effect, the F value for block is not significant at the 5% level (1.196 compard with $F_{4,8,0.05} = 3.8378$) therefore there is no significant difference among the litters and the crb can be used just as well.

表 5.5　Binomial Probability Tables

Tabulated values are $P(Y = a \mid n)$

n = 5

	P												
a	.01	.05	.10	.20	.30	.40	.50	.60	.70	.80	.90	.95	.99
0	.951	.774	.59	.328	.168	.078	.031	.10	.002	0	0	0	0
1	.048	.203	.329	.409	.360	.259	.157	.077	.029	.007	0	0	0
2	.001	.022	.072	.205	.309	.346	.312	.230	.132	.051	.009	.001	0
3	0	.001	.009	.051	.132	.230	.312	.346	.309	.205	.072	.022	.001
4	0	0	0	.007	.029	.077	.157	.259	.36	.409	.329	.203	.05
5	0	0	0	0	.002	.01	.031	.078	.168	.328	.59	.774	.951

n = 10

	P												
a	.01	.05	.10	.20	.30	.40	.50	.60	.70	.80	.90	.95	.99
0	.904	.599	.349	.107	.028	.006	.001	0	0	0	0	0	0
1	.092	.315	.387	.269	.121	.040	.01	.002	0	0	0	0	0
2	.004	.074	.194	.302	.234	.121	.044	.01	.002	0	0	0	0
3	0	.011	.057	.201	.267	.215	.117	.043	.009	.001	0	0	0
4	0	.001	.011	.088	.200	.251	.205	.111	.036	.005	0	0	0
5	0	0	.002	.027	.103	.201	.206	.201	.103	.027	.002	0	0
6	0	0	0	.005	.036	.111	.205	.251	.200	.088	.011	.001	0
7	0	0	0	.001	.009	.043	.117	.215	.267	.201	.057	.011	0
8	0	0	0	0	.002	.01	.044	.121	.234	.302	.194	.074	.004
9	0	0	0	0	0	.002	.01	.04	.121	.269	.387	.315	.092
10	0	0	0	0	0	0	.001	.006	.028	.107	.349	.599	.904

六、鯷魚（ Anchovy ）魚卵和仔魚之成長（ Growth ）

6.1 魚卵和仔魚養殖實驗（ Lo 1983 ）

在過去十年間，西南中心先後於 1976 和 1981 年作了兩次實驗，蒐集鯷魚魚卵和仔魚成長的資料，以擬定其成長模式。在此章中我們將介紹 1981 年實驗之概況與其資料分析之步驟。

在 1981 年實驗中，母魚利用人工催熟，在 15.8 ℃ 的溫度之下產卵，新生之魚卵即被轉移到三個 10 公升的魚缸中，溫度分別是 13.5，15，和 16.5 ℃ 。每一個鐘頭取出約二十粒魚卵，以鑑定其發育期（ Developmental stage ）。在魚卵孵化（ Hatching ）之後，每四小時取出廿條仔魚，十條用以量標準體長（ Standard length ）。因爲魚卵通常飄在水面，仔魚在水中，所以水面和水中層的溫度皆有記錄。

資料記載

溫　度 （ Temperature ）	仔　魚 （ Larval length for larval growth ）	魚　卵 （ Egg stage ）
Date	Date	Date
Elapsed time	Elapsed time	Elapsed time
（ day, hour ）	（ day, hour ）	（ days from hatching, hour ）
Sample time	Sample time	Sample time
Begin	Number of larvae	Stage I
End	Mean length	II
Midpoint	SD	III
Sample type		IV
（ eggs or		.
larvae ）		.
Surface temp.		.
Middle temp.		XI
		Disintegrated
		Total

6.2 魚卵發育（ Development of anchovy eggs ）

A、魚卵發育階段

鯷魚之魚卵（長軸 1.23～1.55 mm，短軸 0.65 ～ 0.82 mm ）之孵化時間（ Incubation time ; t_i ）是因溫度（ Temp. ）而異，在 15 ℃時是 2.5 天（ Lo 1983 ）， t_i 是溫度的降冪數函數。

$$t_i = [\,18.726e^{-0.125\text{temp}}\,] \qquad (6.1)$$

公式（6.1）的參數是根據下列資料推算出來的。

溫度℃	13.9	16.2	15.2	13.8	15.2	16.6	18.0	19.4	20.8	11.1	12.5
孵化時間											
日	3.03	2.51	2.89	3.33	2.63	2.29	2.04	1.67	1.5	4.71	4.08
小時	72.6	60.3	69.5	80	63	55	49	40	36	113	98
	1981 Lab. Experiment			1976 Lab Experiment							

在孵化期間，卵的發育被分十一個階段（Moser and Ahlstrom 1985）。達到每一階段的時間因溫度而異，從 1981 Lab. 實驗可以推算在三種不同溫度下達到各個階段所需的時間（表 6.1）。1981 年資料連同 1976 年資料一起用於選擇魚卵發育模式（Lo 1985）。此模式應用之一是鑑定卵的年齡，更進一步的是推算魚卵的死亡率。

B、魚卵發育模式（Lo 1985）

表 6.1（Lo 1985）列出在不同溫度下魚卵達到任何一階段所需時間（小時）。

表 6.1 Average age (In hours. minutes) ($y_{i,t}$) of northern anchovy eggs for each of 10 developmental stages (i) (Stage I was not observed) at various temperatures ℃ (t) from laboratory experiments conducted at the SWFC.

	1981 Laboratory Data (Lo 1983)			Zweifel & Lasker (1976)					
Temperature ℃ (t)	13.9	15.2	16.2	13.8	15.2	16.6	18.0	19.4	20.8
Stage (i)									
Ⅱ	6.82	6.42	6.40						
Ⅲ	16.36	13.55	13.14	20	15	10	9	8	6
Ⅳ	24.91	21.12	20.18						
Ⅴ	35.88	30.7	25.56						
Ⅵ	44.63	39.24	33.20	42	35	26	24	21	9
Ⅶ	49.64	47.13	38.56						
Ⅷ	52.5	52.07	43.64						
Ⅸ	61.1	56.28	50.48	58	50	39	35	33	28
Ⅹ	66.09	62.63	54.78						
Ⅺ	69.79	65.65	56.10	78	65	55	44	39	35

$$y_{i,t} = f(i, t)$$

i：階段，t：溫度℃，$y_{i,t}$：是在溫度 t℃時達到 i 階段所須之時間。

在 i^{th} 階段中 $$y_{i,t} = a_i e^{b_i t} \qquad (6.2)$$

所以 $y_{i,t}$ 是溫度的冪數函數。

在 t℃中 $$y_{i,t} = a_t e^{b_t i} i^{c_t} \qquad (6.3)$$

因此最後的模式變成

$$y_{i,t} = a e^{(b_i t + b_t i)} i^{c_t} = 16.07 e^{-(0.1145t + 0.098i)} i^{1.74} \qquad (6.4)$$

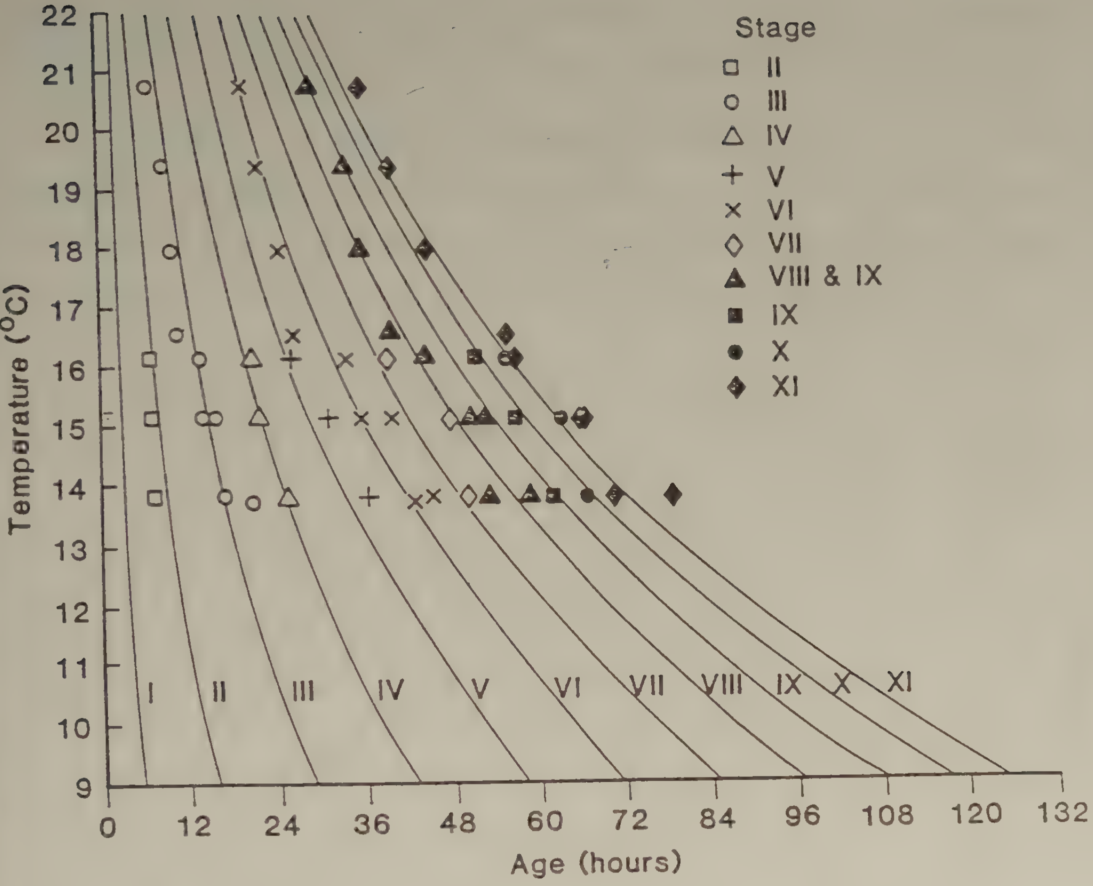


圖 6.1. Observed (denoted by various symbols) and predicted (smooth lines) of time-to-the ith stage as a function of temperature (°C) based upon egg development data collected from two laboratory experiments conducted at SWFC. The predicted values are computed from equation (4).

C、魚卵發育模式應用之一：決定魚卵年齡。

運用圖 6.2（ Lo 1985 ）和拖網時間可以決定魚卵的年齡，這是因爲鯷魚（ Anchovy ）產卵時間短暫，估計在 1800 － 0200 ，高峯是在 2200 。此種方法不適合應用於 24小時連續產卵的魚類。

根據圖 6.2 ，所有在 1800 –0200 觀察的魚卵被列爲新產魚卵（ s ），以後 24 小時的魚卵（ 0200 － 0159 ）是列爲天 0 ，天 1 ，天 2 ，天 3 卵（ A－day ，B－day ，C－day ，D－day ）例如在溫度 16 ℃，晚上 6 點（ 1800 ）收集的魚卵的估計年齡應爲

Stage	Ⅰ	Ⅱ	Ⅲ	Ⅳ	Ⅴ	Ⅵ	Ⅶ	Ⅷ	Ⅸ	Ⅹ	Ⅺ
Age	S	—	A	A	A	B	B	B	B	B	B , C

Day	S	0	0	0	1	1	1	1	1	1，2
Hour		20	20	20	44	44	44	44	44	44，68

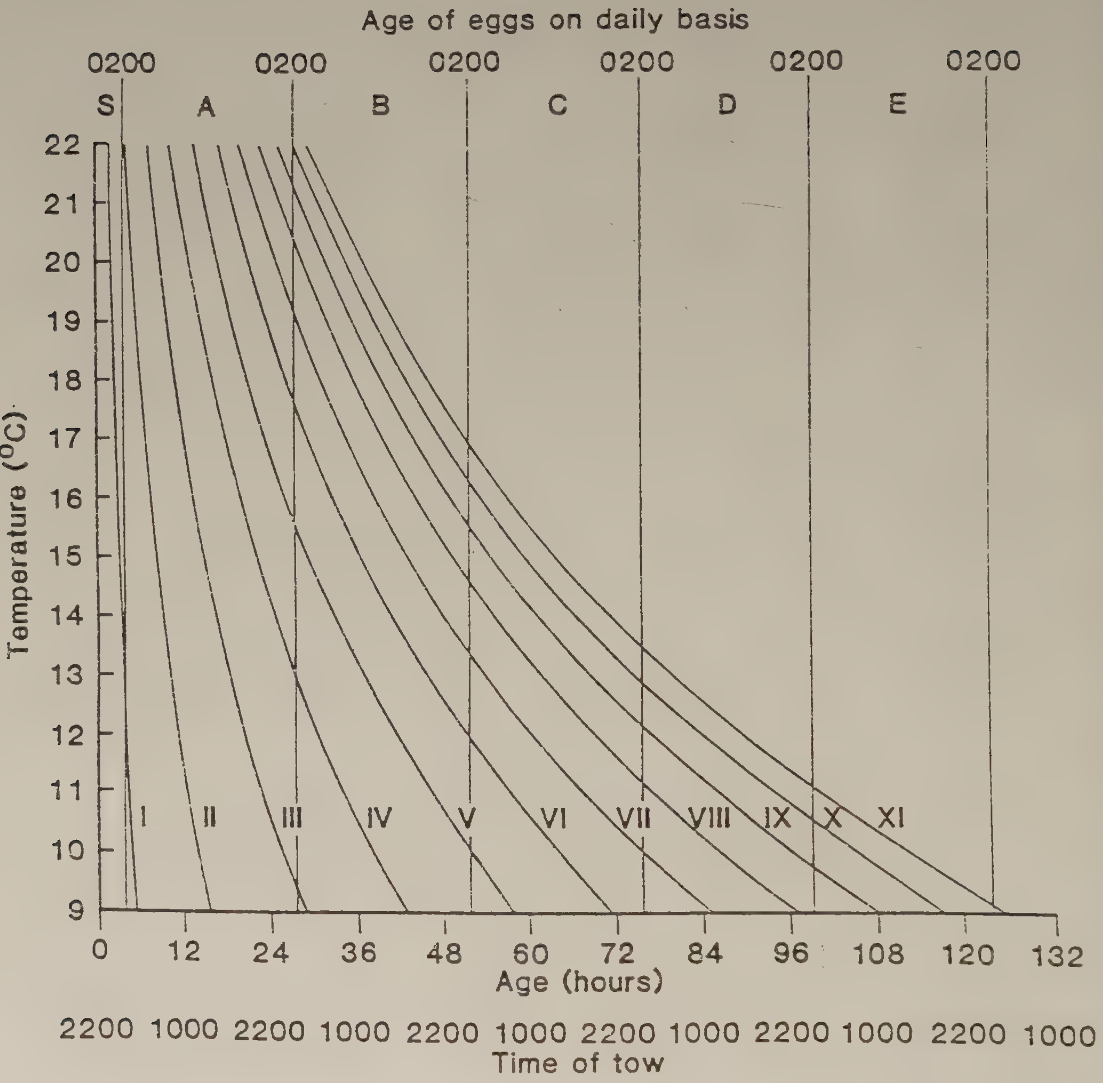


圖 6.2. Function relationship of average age of eggs for the ith stage based upon time of the tow and sea surface temperature (°C).

6.3 推算魚卵年齡之電腦制度（ Automated system ）

因爲所有資料：拖網時間，水溫度，魚卵發育階段的次數（ Frequency ）都貯藏在

電腦中，推算魚卵年齡程序可以自動化。運用下列公式，先立一個參考表，表中列出魚卵階段（i），拖網時間（k）（00:00－23:59），溫度（t）的魚卵年齡（$y_{i,t,k}$）。

$y_{i,t}$ 自公式（6.4）計算來的是平均值。如果魚卵只出現在預期時間 $\hat{T}$（$\hat{T}=\frac{y_{i,t}+ST}{24}$ 的餘數，ST 是產卵時間（2200）），則可直接運用公式（6.4）。但是不同階段的魚卵出現於不同時間，所以 $y_{i,t}$ 是不夠用的。簡單而言，如果魚卵在 $\hat{T}$ 小時前被捕，則其年齡應比 $y_{i,t}$ 要小，反之亦然。根據此理，如果魚卵在 k 小時被捕，則其年齡應爲

$$y_{i,t,k}=y_{i,t}+k-\hat{T}$$

但 $y_{i,t,k}$ 應在 $y_{i,t}\pm 2SD_{i,t}$（$SD_{i,t}$ 是年齡 $y_{i,t,k}$ 的標準差）

$$\therefore \text{ if } \quad |k-\hat{T}|\leqslant 2SD_{i,t}$$

$$y_{i,t,k}=y_{i,t}+k-\hat{T}$$

$$\text{if } \quad |k-\hat{T}|>2SD_{i,t}$$

$$y_{i,t,k}=y_{i,t}\pm 2SD_{i,t}$$

$$\text{But} \quad y_{i,t,k}\geqslant 0 \qquad \therefore \quad y_{i,t}\geqslant 2SD_{i,t}$$

所以我們再用一個變數

$$G=\begin{cases}2SD_{i,t} & y_{i,t}>2SD_{i,t}\\ y_{i,t} & y_{i,t}<2SD_{i,t}\end{cases}$$

$$y_{i,t,k}=\begin{cases}y_{i,t}-G & k<\hat{T}-G\\ y_{i,t}+k-\hat{T} & \hat{T}-G<k<\hat{T}+G\\ y_{i,t}+G & \hat{T}+G<k\end{cases}$$

（表 6.2）（Lo 1985）

最後所有的魚卵均歸併於 S，A，B，C day：S（0－3h），A（4－27h），B（28－51h），C（52－75h），D（76－99h）。（表 6.3）（Lo 1985）

魚卵的年齡的次數（Frequency）可以用作推算魚卵的死亡率。（表 6.4）（Lo 1985）

6.4 魚苗之成長（Growth of anchovy larvae）

A、成長曲線概論（Draper and Smith 1981）

成長曲線，理論上是根據長成率的微分方程（Differential equation）演變出來的。成長曲線不只用於描述魚體長和體重的成長，亦用於推算整個魚族群的成長。

如果 y_t 是魚在年齡 t 的體長，瞬間成長率（Instantaneous growth rate），g(t)

$=\frac{dy_t}{dt}\cdot\frac{1}{y_t}$ 。幾種常用之生長模式列舉如下：

瞬間成長率（g(t)）	生長模式	
α	$y_t = y_0 e^{\alpha t}$	Exponential
$\alpha\left[\left(\frac{y_\infty}{y_t}\right)^\beta - 1\right]$	$y_t = y_\infty\left(1 - k e^{-\alpha\beta t}\right)^{\frac{1}{\beta}}$	von Bertalanffy
$\alpha\left[1 - \left(\frac{y_t}{y_\infty}\right)^\beta\right]$	$y_t = y_\infty\left(1 + \beta e^{-\alpha\beta t}\right)^{-\frac{1}{\beta}}$	Richards
$\alpha\left[1 - \frac{y_t}{y_\infty}\right]$	$y_t = y_\infty\left(1 + e^{k-\alpha t}\right)^{-1}$	Logistic
$\alpha e^{-\beta t}$	$y_t = y_\infty e^{-\frac{\alpha}{\beta} e^{-\beta t}}$	Gompertz

B、鯷魚仔魚成長模式

鯷魚仔魚之成長模式是分成兩個階段來研究的，在卵黃囊期（ Yolk－sac ），仔魚成長是因溫度而異，成長資料來自實驗室養殖之仔魚。但自攝食（ First feeding ; FF ）之後，溫度的影響似乎被其它環境因素所掩蓋而不顯著，成長資料來自海中採取的樣本。

我們用兩個公式分別代表 Yolk－sac 和攝食以後的成長模式，成長模式是採用 Gompertz 公式

$$L_t = L_\infty\left(\frac{L_k}{L_\infty}\right)^{\mathrm{EXP}\{-\alpha(t-t_k)\}}$$

$$= L_\infty e^{\ln\left(\frac{L_k}{L_\infty}\right)\mathrm{EXP}\{-\alpha(t-t_k)\}} \qquad (6.5)$$

L_t 是自卵受精後 t 日的魚體長

t_k 是在考慮之年齡期間的最小年齡（日）

L_k 是在年齡 t_k 日時的魚體長

α 是成長係數

L_∞ 是考慮之年齡期間之最大魚體長

公式（6.5）是從瞬間成長率演變出來的

$$\frac{dL_t}{dt}\cdot\frac{1}{L_t} = \lambda e^{-\alpha(t-t_k)}$$

λ 是在年齡 t_k 時的瞬間成長率

a、卵黃囊期的成長模式（ Up to 5 days old ）

仔魚在此期間之成長與溫度有關，所以我們先考慮各溫度下之成長資料來估計成長曲線的參數：在此階段 t_k（最小年齡）是孵化時間（ Hatching time ），孵化時間又

表 6.2 Partial listing of the look-up table. Each entry is the estimated age (in hours.minutes) for stage IV for each combination of time of tow (1 to 24 hours) and temperature (10 to 22 ℃). The asterisk (*) indicates the estimated age corresponding to the expected time of tow ($\hat{T}$) (see Tables 2 a & 2 b, Lo 1983). Row 25 is for random assignment of ages for eggs observed at 12 hours before or after the expected time of tow.

Time of tow	Temperature (°C)												
(k)	10	11	12	13	14	15	16	17	18	19	20	21	22
1	28.25	27.28	27.57	27.50	27.02	27.32	26.19	24.20	6.34	4.60	3.35	3.20	3.13
2	28.25	28.28	28.57*	28.50	28.02	28.32	26.19	8.20	6.34	4.60	4.35	4.20	4.13
3	29.25	29.28	29.57	29.50	29.02	28.32	26.19	8.20	6.34	5.60	5.35	5.20	5.13
4	30.25	30.28	30.57	30.50	30.02	28.32	10.19	8.20	6.34	6.60	6.35	6.20	6.13
5	31.25	31.28	31.57	31.50	31.02	28.32	10.19	8.20	7.34	7.60	7.35	7.20	7.13
6	32.25	32.28*	32.57	32.50	31.02	12.32	10.19	8.20	8.34	8.60	8.35	8.20	8.13
7	33.25	33.28	33.57	33.50	31.02	12.32	10.19	9.20	9.34	9.60	9.35	9.20	9.13*
8	34.25	34.28	34.57	33.50	31.02	12.32	10.19	10.20	10.34	10.60	10.35	10.20*	10.13
9	35.25	35.28	35.57	33.50	15.02	12.32	11.19	11.20	11.34	11.60	11.35*	11.20	11.13
10	36.25*	36.28	36.57	33.50	15.02	12.32	12.19	12.20	12.34	12.60*	12.35	12.20	12.13
11	37.25	37.28	36.57	17.50	15.02	13.32	13.19	13.20	13.34	13.60	13.35	13.20	13.13
12	38.25	38.28	36.57	17.50	15.02	14.32	14.19	14.20	14.34*	14.60	14.35	14.20	14.13
13	39.25	39.28	36.57	17.50	15.02	15.32	15.19	15.20	15.34	15.60	15.35	15.20	15.13
14	40.25	40.28	20.57	17.50	16.02	16.32	16.19	16.20*	16.34	16.60	16.35	16.20	16.13
15	41.25	40.28	20.57	17.50	17.02	17.32	17.19	17.20	17.34	17.60	17.35	17.20	17.13
16	42.25	40.28	20.57	18.50	18.02	18.32	18.19*	18.20	18.34	18.60	18.35	18.20	17.13
17	43.25	40.28	20.57	19.50	19.02	19.32	19.19	19.20	19.34	19.60	19.35	18.20	17.13
18	44.25	24.28	20.57	20.50	20.02	20.32*	20.19	20.20	20.34	20.60	19.35	18.20	17.13
19	44.25	24.28	21.57	21.50	21.02	21.32	21.19	21.20	21.34	20.60	19.35	18.20	1.13
20	44.25	24.28	22.57	22.50	22.02	22.32	22.19	22.20	22.34	20.60	19.35	2.20	1.13
21	44.25	24.28	23.57	23.50	23.02*	23.32	23.19	23.20	22.34	20.60	3.35	2.20	1.13
22	28.25	24.28	24.57	24.50	24.02	24.32	24.19	24.20	22.34	4.60	3.35	2.20	1.13
23	28.25	25.28	25.57	25.50*	25.02	25.32	25.19	24.20	22.34	4.60	3.35	2.20	1.13
24	28.25	26.28	26.57	26.50	26.02	26.32	26.19	24.20	6.34	4.60	3.35	2.20	2.13
25	44.25	40.28	36.57	33.50	31.02	28.32	26.19	24.20	22.34	20.60	19.35	18.20	17.13

表 6.3 Partial listing of the output data file (FOR026.DAT) for 1983: Cruise identification, tow time, temperature, number of eggs and estimated ages (in hours) grouped by S(0-3 h), A(4-27 h), B(28-51 h), C(52-75 h), D(76-99 h) and total number for each tow. Disintegrated eggs are obtained by subtraction. E day eggs (100-123 h) are not observed for northern anchovy and thus are not included in the output.

Cruise No.	Tow No.	CalCOFI Line	CalCOFI Station	Stratum	Weighting Factor	Date	Region	Tow Time		Temperature °C	Day Categories*										Total
											S		A		B		C		D		
302	17	741	550	1	1.000	830205	1	23	28	14	0.	1.	1.	25.	0.	48.	0.	71.	0.	0.	1.
302	18	741	540	1	1.000	830206	1	24	20	14	0.	2.	0.	20.	1.	50.	0.	71.	0.	0.	1.
302	19	741	530	1	1.000	830206	1	1	13	14	0.	3.	0.	20.	3.	51.	0.	65.	0.	0.	3.
302	24	750	485	1	1.000	830206	1	6	19	14	0.	0.	0.	7.	0.	37.	0.	58.	0.	0.	0.
302	26	750	500	1	1.000	830206	1	15	39	15	0.	0.	0.	16.	0.	41.	2.	62.	0.	0.	2.
302	27	750	510	1	1.000	830206	1	17	17	15	0.	2.	0.	19.	0.	43.	0.	64.	0.	0.	0.
302	29	750	520	1	1.000	830206	1	22	32	15	0.	2.	0.	24.	0.	48.	0.	66.	0.	0.	0.
302	30	750	530	1	1.000	830206	1	23	11	14	0.	1.	0.	19.	0.	48.	0.	71.	0.	0.	0.
302	31	750	540	1	1.000	830207	1	24	8	14	0.	2.	0.	20.	2.	50.	0.	71.	0.	0.	3.
302	32	750	550	1	1.000	830207	1	24	49	14	0.	2.	0.	20.	0.	49.	2.	69.	0.	0.	2.
302	33	750	560	1	1.000	830207	1	1	47	14	0.	3.	0.	20.	0.	46.	2.	57.	0.	0.	2.
302	34	750	570	1	1.000	830207	1	2	31	14	0.	0.	0.	5.	0.	34.	1.	57.	0.	0.	1.
302	38	758	600	1	1.000	830207	1	6	16	14	0.	0.	0.	7.	0.	37.	2.	56.	0.	0.	2.
302	39	758	590	1	1.000	830207	1	7	20	14	0.	0.	0.	7.	0.	34.	2.	57.	0.	0.	2.
302	40	758	580	1	1.000	830207	1	8	7	14	0.	0.	0.	8.	0.	35.	2.	58.	0.	0.	2.
302	41	758	570	1	1.000	830207	1	8	52	14	0.	0.	0.	8.	0.	35.	0.	59.	0.	0.	0.
302	42	758	560	1	1.000	830207	1	9	34	14	0.	0.	0.	10.	0.	36.	0.	59.	0.	0.	0.
302	43	758	550	1	1.000	830207	1	10	39	14	0.	0.	0.	11.	0.	37.	2.	60.	0.	0.	2.
302	44	758	540	1	1.000	830207	1	11	22	14	0.	0.	0.	11.	0.	38.	2.	61.	0.	0.	2.
302	45	758	530	1	1.000	830207	1	12	0	15	0.	0.	0.	13.	1.	38.	1.	62.	0.	0.	2.
302	46	758	520	1	1.000	830207	1	12	35	15	0.	0.	0.	13.	0.	38.	3.	61.	0.	0.	3.
302	47	758	510	1	1.000	830207	1	13	16	15	0.	0.	0.	15.	0.	40.	0.	63.	0.	0.	0.
302	49	758	495	1	1.000	830207	1	14	30	15	0.	0.	0.	16.	0.	40.	0.	63.	0.	0.	0.
302	50	767	480	1	1.000	830207	1	17	9	15	0.	0.	0.	17.	0.	43.	0.	64.	0.	0.	0.
302	51	767	490	1	1.000	830207	1	18	28	15	0.	2.	0.	20.	1.	44.	0.	64.	0.	0.	1.
302	52	767	500	1	1.000	830207	1	20	46	15	0.	2.	0.	23.	0.	47.	0.	66.	0.	0.	0.
302	53	767	510	1	1.000	830207	1	22	25	15	0.	2.	3.	24.	1.	48.	0.	66.	0.	0.	4.
302	54	767	520	1	1.000	830208	1	24	43	15	0.	3.	0.	21.	0.	49.	0.	54.	0.	0.	0.
302	55	767	530	1	1.000	830208	1	1	31	15	0.	3.	0.	22.	0.	50.	0.	54.	0.	0.	0.
302	56	767	540	1	1.000	830208	1	2	17	15	0.	0.	0.	4.	1.	28.	0.	53.	0.	0.	1.
302	57	767	550	1	1.000	830208	1	3	6	15	0.	0.	1.	5.	1.	29.	0.	53.	0.	0.	2.
302	58	767	560	1	1.000	830208	1	5	28	15	0.	0.	0.	6.	1.	31.	0.	54.	0.	0.	1.
302	59	767	570	1	1.000	830208	1	6	22	14	0.	0.	0.	7.	1.	32.	0.	58.	0.	0.	1.
302	64	775	590	1	1.000	830208	1	14	14	14	0.	0.	0.	15.	1.	38.	0.	64.	0.	0.	1.
302	65	775	580	1	1.000	830208	1	14	53	14	0.	0.	0.	15.	0.	41.	0.	64.	0.	0.	0.
302	66	775	570	1	1.000	830208	1	15	29	15	0.	0.	0.	16.	0.	41.	1.	62.	0.	0.	1.
302	67	775	560	1	1.000	830208	1	16	15	15	0.	0.	0.	17.	1.	42.	1.	66.	0.	0.	2.
302	68	775	550	1	1.000	830208	1	17	3	14	0.	0.	0.	18.	0.	44.	0.	67.	0.	0.	0.

*Under each day category are number of eggs and age (in·hours).

表 6.4

Partial listing of the data file (FOR038.DAT):
Cruise ID, number of eggs and age (in days)
excluding eggs older than 2.5 days old.

Cruise No.	Tow No.	CalCOFI Line	CalCOFI Station	Date	Number of Eggs	Age (in days)
302	6	0733	0550	830205	0.0000	0.4583
302	6	0733	0550	830205	0.0000	1.5694
302	6	0733	0550	830205	1.0000	2.5417
302	17	0741	0550	830205	1.0000	1.0417
302	17	0741	0550	830205	0.0000	2.0104
302	17	0741	0550	830205	0.0000	2.9583
302	18	0741	0540	830206	0.0000	0.8229
302	18	0741	0540	830206	1.0000	2.0833
302	18	0741	0540	830206	0.0000	2.9583
302	19	0741	0530	830206	0.0000	0.3438
302	19	0741	0530	830206	3.0000	2.1250
302	19	0741	0530	830206	0.0000	2.7083
302	24	0750	0485	830206	0.0000	0.2778
302	24	0750	0435	830206	0.0000	1.5208
302	24	0750	0485	830206	0.0000	2.3958
302	26	0750	0500	830206	0.0000	0.6667
302	26	0750	0500	830206	0.0000	1.7083
302	26	0750	0500	830206	2.0000	2.5833
302	27	0750	0510	830206	0.0000	0.7917
302	27	0750	0510	830206	0.0000	1.7813
302	27	0750	0510	830206	0.0000	2.6667
302	29	0750	0520	830206	0.0000	0.9896
302	29	0750	0520	830206	0.0000	2.0000
302	29	0750	0520	830206	0.0000	2.7500
302	30	0750	0530	830206	0.0000	0.8021
302	30	0750	0530	830206	0.0000	2.0104
302	30	0750	0530	830206	0.0000	2.9583
302	31	0750	0540	830207	0.0000	0.8229
302	31	0750	0540	830207	2.0000	2.0833
302	31	0750	0540	830207	0.0000	2.9583
302	32	0750	0550	830207	0.0000	0.8229
302	32	0750	0550	830207	0.0000	2.0417
302	32	0750	0550	830207	2.0000	2.8750
302	33	0750	0560	830207	0.0000	0.8438
302	33	0750	0560	830207	0.0000	1.9063
302	33	0750	0560	830207	2.0000	2.3750
302	34	0750	0570	830207	0.0000	0.2083
302	34	0750	0570	830207	0.0000	1.4271
302	34	0750	0570	830207	1.0000	2.3750
302	38	0758	0600	830207	0.0000	0.2778
302	38	0758	0600	830207	0.0000	1.5208
302	38	0758	0600	830207	2.0000	2.3333
302	39	0758	0590	830207	0.0000	0.3056
302	39	0758	0590	830207	0.0000	1.4167
302	39	0758	0590	830207	2.0000	2.3750
302	40	0758	0580	830207	0.0000	0.3333
302	40	0758	0580	830207	0.0000	1.4375

是因溫度而異（見魚卵發育6.2 節），一共有 6 種不同的溫度，三個是在 1981年實驗中的溫度，其它三個溫度是以前實驗結果（ Lo 1983 ）。

Temp, ℃	L_∞(mm)	L_k (mm)	α	n	t_k (hatching time ; days)
13.47	4.166	3.11	0.551	30	3.48
14.00	4.21	2.27	0.78	7	3.25
15.03	4.328	2.86	0.556	30	2.86
16.23	4.287	2.84	0.9438	11	2.46
17.00	4.546	2.406	1.1543	8	2.24
20.00	4.152	2.40	1.71	10	1.54

在三個參數中 L_k 和 α （成長係數）受溫度的影響，α 是最敏感的，所以我們決定將 α 寫成溫度的函數。在決定最後曲線時 $t_0=0$ ，L_0是不受溫度影響，但本身無任何生物上的意義。

$$\alpha_{temp}=0.11\,e^{0.12\,(temp)}$$

最後的模式是

$$L_t=4.25\,(\frac{0.32}{4.25})\,e^{-0.11\,e^{0.12\,(temp.)}\,(t-t_0)} \qquad \text{for } t<6.3 \text{ days}$$

（圖 6.3 ）（ Lo 1983 ）

b 、仔魚〔4.1 mm－27 mm ；＞6 days old (FF)〕的成長模式（ Methot and Kramer 1979 ; Methot and Hewitt 1980 ）。

資料收集：資料來自 1976－1979 海上調查（ 1976 ：三，五月； '77 ：三月； '78 ：一，四，五，八月； '79 ：一月）。用的魚網有 1 米圈網（ 1m Ring net ），Bongo net （ 60cm 直徑）和 Manta Neuston net 。網目大小皆爲 505 μm ，自不同的深度斜拖網。樣本是保存在 85 ％ Ethanol （氨基乙醇），海面溫度亦記錄下來，資料收集地點是南加州海灣： Anchovy 產卵主要地區之內。

收集的魚卵和仔魚都經分類。魚體長是量自吻部（ Snout ）的尖端。尺度準確到 0.1 mm 。矢石（ Sagittae ）被移出而放在顯微鏡下，平的一面朝上。偏光濾波器和偏光鏡（ Polarizing filter & Analyser ）用於顯微鏡之下使耳骨更顯明。切片晾乾後放在一片蓋玻片之下（ Pro－texx ），在影像銀幕（ Video screen ）上的骨片，用以數算骨輪，顯微鏡放大量是 600× 或 1500× 。每一耳骨皆有一到三個觀測值。三個數目的平均數用以推算此耳骨的骨輪，骨輪是用來表示卵黃囊吸收後的日數年齡。

仔魚（ After FF ）的成長曲線之成長係數似乎是因月份而變，與溫度之關係不顯

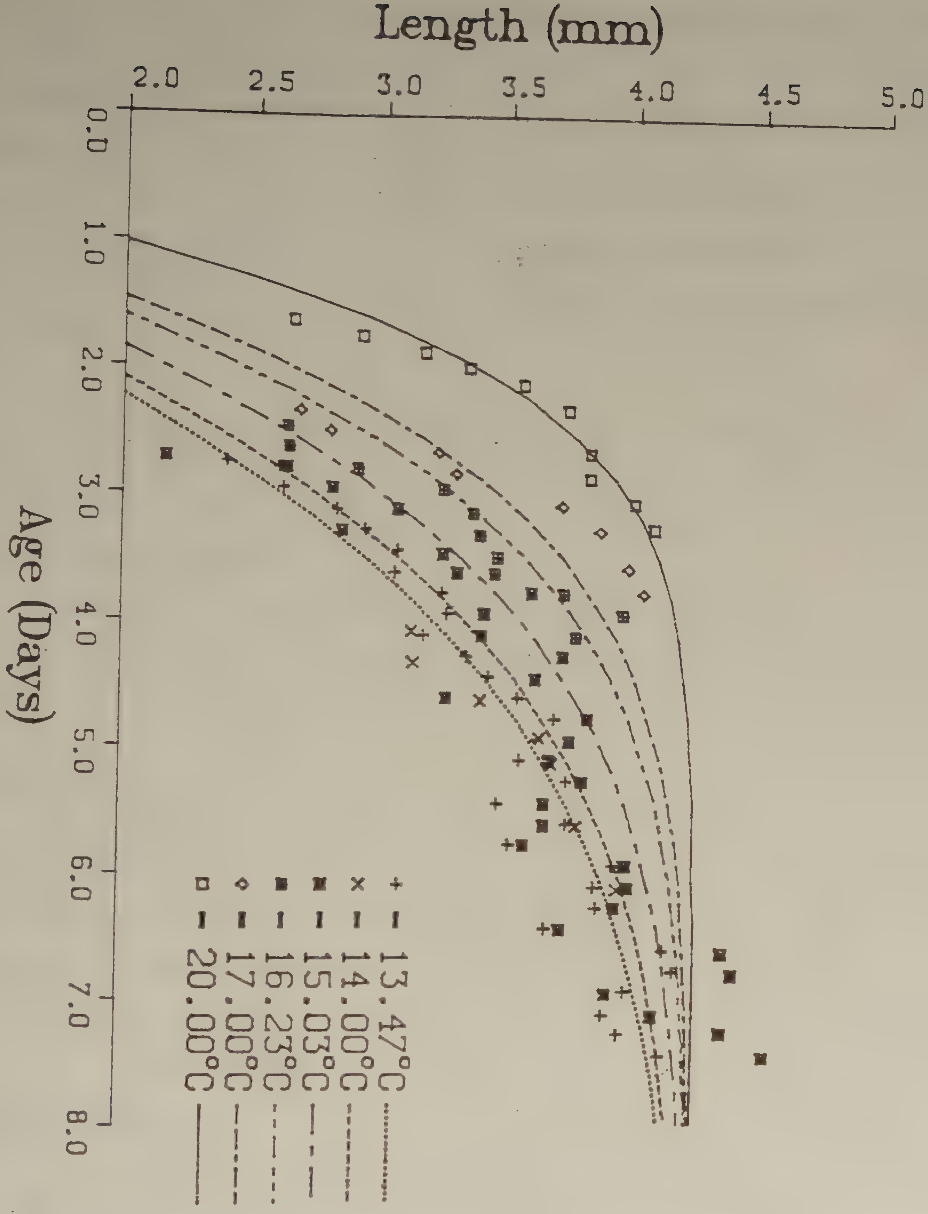


圖 6.3. Growth curves of yolk-sac stage of anchovy larvae at various temperatures.

著。以下是因月份而異之仔魚成長率推算值（α）：

月份	一	二	三	四	五	六	七	八
α	0.0462	0.0481	0.0501	0.0523	0.0547	0.0573	0.0602	0.0634

$$\alpha_{\text{month}} = [22.4786 - 0.8374\,(\text{month})]^{-1}$$

攝食後仔魚之成長模式爲：

$$L_t = 27\left(\frac{4.1}{27}\right)^{e^{-\alpha_{\text{month}}\cdot(t-6.28)}} \qquad \text{for } 6.3 < t < 60 \text{ days}$$

七、鯷魚（Anchovy）魚卵和仔魚之死亡（Mortality）推算

7.1 資料收集與處理

資料收集是由 California Cooperative Oceanic Fisheries Investigation（CALCOFI）每年調查所得的。CALCOFI 是一個由美國商務部（National Marine Fisheries Service, Department of Commerce）、加州大學 Scripps Institute of Oceanography，和加州漁獵部合作的研究組織。調查範圍包括 20°N 到 40°N，110°W 到 130°W。調查站是按觀測線設置的，每一條線上有固定的測站，每一站上分別用兩種不同的浮游生物網來捕獲魚卵和仔魚（圖 7.1）。

A、魚網

a、魚卵垂直魚網（Calvet：California vertical net）：架圈的直徑爲 0.25m，網長 1.5m，表面面積爲 0.05 m^2，濾水面積（Filtering surface）是 0.87 m^2，尼龍 Nitex 魚網之網目大小是 0.150mm。操作程序是以 70m/min 速度達到深度 70m 時，停留 10 秒鐘再以 70m/min 速度將網收回。

b、仔魚 Bongo net：是無支索的浮游生物網（Bridle－free plankton net）。Bongo net 長 3.4m 具有兩個直徑 0.71m 圓形鋁架。由一個中心軛所聯接，再接上曳網，在鋁圈下裝一個 22 公斤的重錘，使網能被斜拖（Oblique tow）。曳速是 50m/min（Smith 1977）。

B、資料記載

每一拖網均須塡寫一拖網資料表（Tow－Data sheet）（圖 7.2），其中項目甚多，爲了計算產卵的魚總量（Spawning biomass），所有魚卵或仔魚數量均須換成一個標準單位（例如 10 m^2）的魚獲量，我們須計算魚網之滲水總量（Volume of H_2O strained）和拖網深度（Depth of tow in meters），換算 10 m^2 之魚獲量公式則爲：

$$X \cdot \frac{10}{\dfrac{\text{Volume of } H_2O}{\text{Depth of tow}}} = X \cdot \text{SHF}$$

X 是實際之魚獲量觀測量

$$\frac{10}{\text{Volume of } H_2O/\text{Depth of tow}} = \text{Standard haul factor} = \text{SHF}$$

Volume of water ＝ a・b

a：Area of month of net

b：Length of tow path

b＝（Meter/Revolution）・（No of revolutions of the flow meter）

Depth of tow ＝ Maximun length of wire out・cos（$\tan^{-1}$ T）

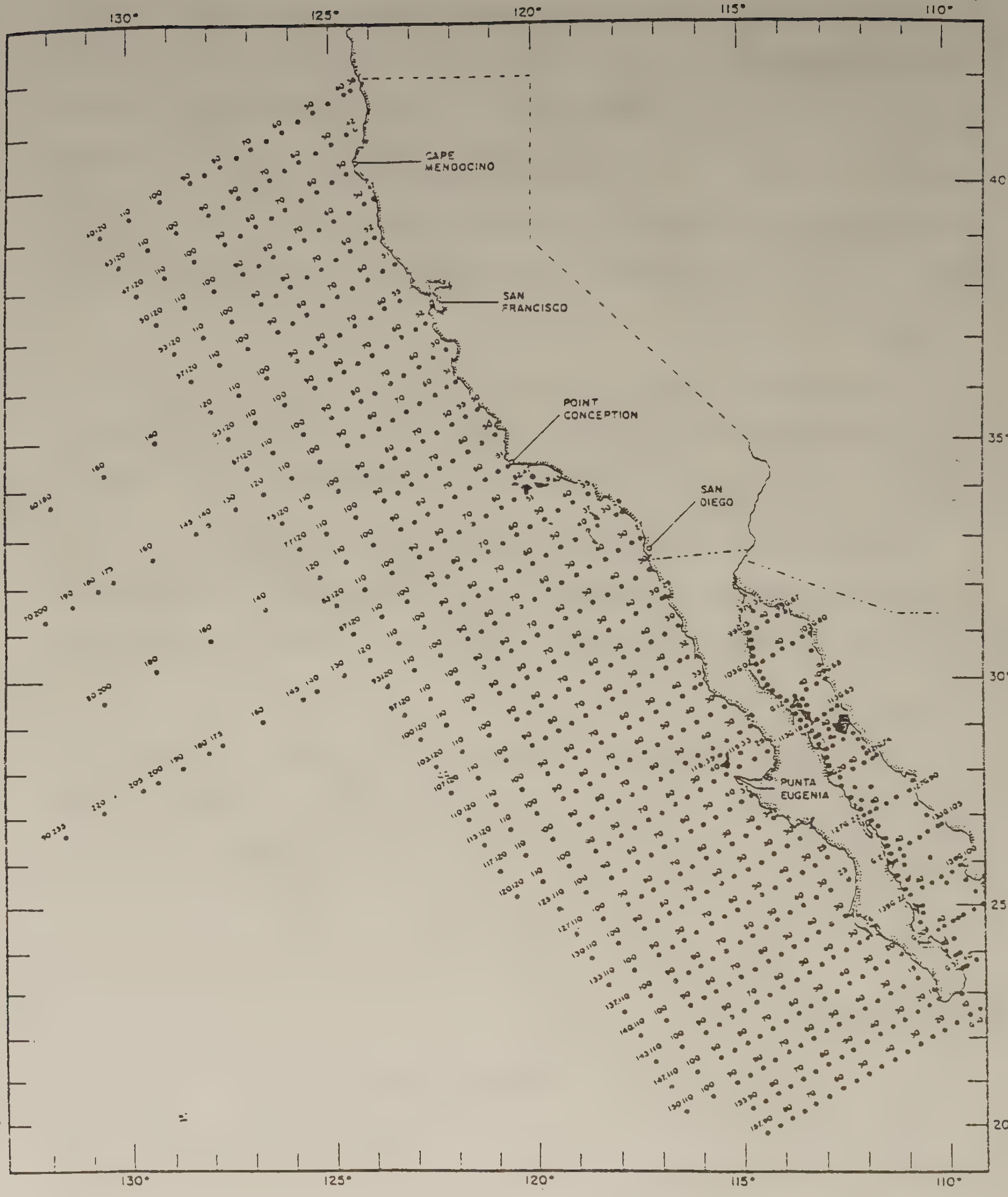
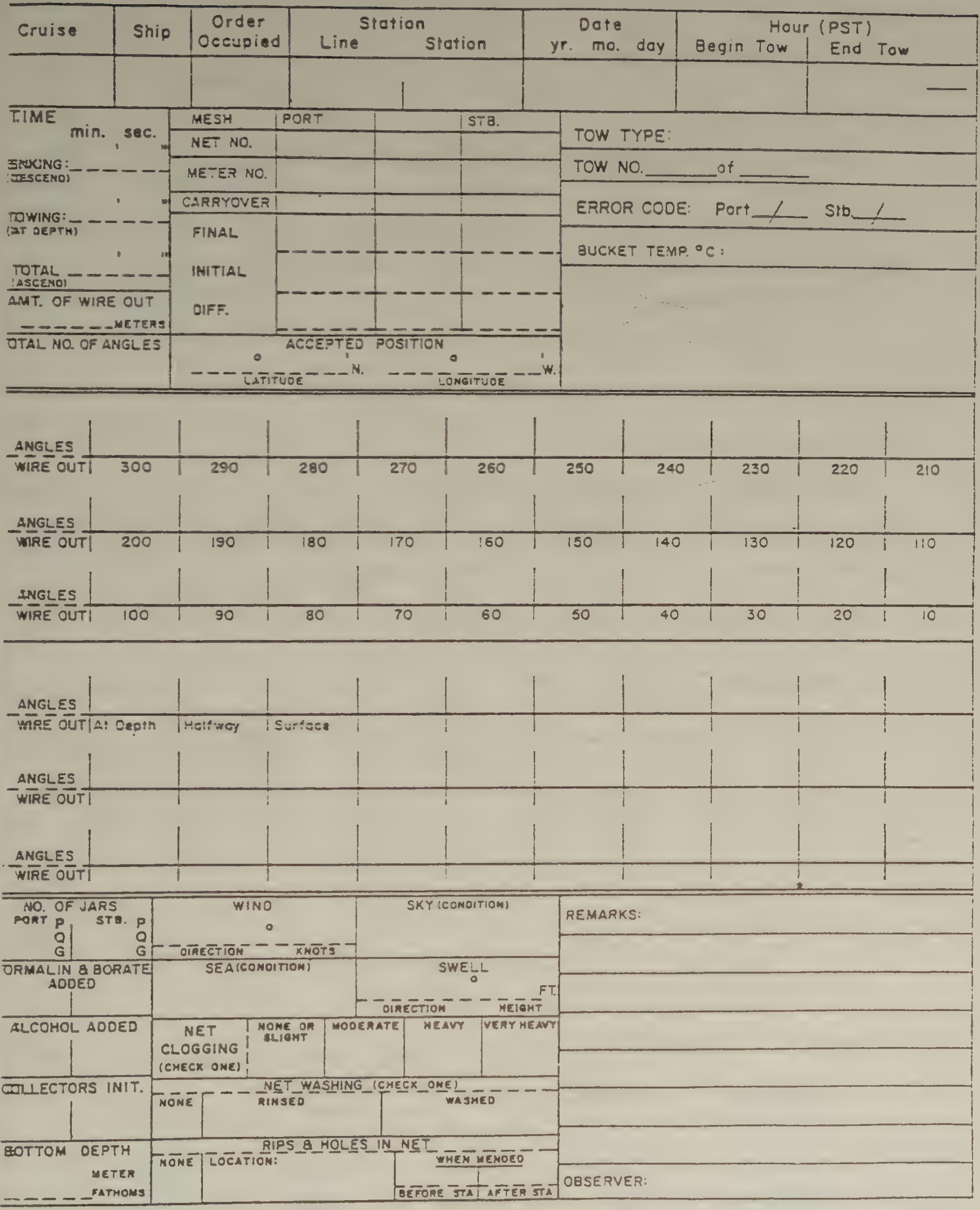

130°
125°
120°
115°
110°
40°
35°
30°
25°
20°
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA

圖 7.1 CALCOFI BASIC STATION PLAN SINCE 1950

圖 7.2 NET TOW DATA SHEET



Cruise	Ship	Order Occupied	Station Line	Station Station	Date yr. mo. day	Hour (PST) Begin Tow	Hour (PST) End Tow

TIME min. sec.
SINKING: ' " (DESCEND)
TOWING: ' " (AT DEPTH)
TOTAL ' " (ASCEND)
AMT. OF WIRE OUT ______ METERS
OTAL NO. OF ANGLES

MESH	PORT		STB.
NET NO.			
METER NO.			
CARRYOVER			
FINAL			
INITIAL			
DIFF.			

ACCEPTED POSITION
___° ___' N. ___° ___' W.
LATITUDE LONGITUDE

TOW TYPE:
TOW NO. ______ of ______
ERROR CODE: Port __/__ Stb __/__
BUCKET TEMP. °C:

ANGLES										
WIRE OUT	300	290	280	270	260	250	240	230	220	210
ANGLES										
WIRE OUT	200	190	180	170	160	150	140	130	120	110
ANGLES										
WIRE OUT	100	90	80	70	60	50	40	30	20	10

ANGLES										
WIRE OUT	At Depth	Halfway	Surface							
ANGLES										
WIRE OUT										
ANGLES										
WIRE OUT										

NO. OF JARS
PORT p Q G STB. p Q G

WIND ° DIRECTION KNOTS

SKY (CONDITION)

REMARKS:

ORMALIN & BORATE ADDED

SEA (CONDITION)

SWELL ° FT.
DIRECTION HEIGHT

ALCOHOL ADDED

NET CLOGGING (CHECK ONE)	NONE OR SLIGHT	MODERATE	HEAVY	VERY HEAVY

COLLECTORS INIT.

NET WASHING (CHECK ONE)

NONE	RINSED	WASHED

BOTTOM DEPTH
METER
______ FATHOMS

RIPS & HOLES IN NET

NONE	LOCATION:	WHEN MENDED BEFORE STA	WHEN MENDED AFTER STA

OBSERVER:

$$\bar{T} = \frac{1}{n} \sum_{i=1}^{n} \tan \theta_i$$

$\begin{cases} \theta \text{ is the wire angle.} \\ n \text{ is the number of } \theta \text{ measured at various wire out.} \end{cases}$ （見圖 7.2 ）

(Smith 1977)

SHF 可用以換算不同漁網收集的資料，例如 Vertical tow 和 Bongo tow 。

C 、資料處理

所有標本帶回試驗所以後，魚卵和仔魚經由分類員（ Sorter ）分類，記錄於 Sorter tally－data 中。魚卵和仔魚數量則經由電腦分別記載於魚卵和仔魚資料庫（ Data base ）中。統計分析則根據此 Data base 中的資料，其它的 Data base 有 1.調查站活動 Data base 2.海洋資料 Data base 3.生物資料 Data base 4. Cruise specification data base 。（圖 7.3 ）。

7.2 魚卵之死亡推算（ Lo 1985 ）

對於一系魚卵，P_t 是年齡 t day 的魚卵數，$t = 0, 1, \cdots\cdots, t_h$ ；t_h 是孵化年齡〔 t_h = 第六章的 t_i （公式 6.1 ）〕，則 $P_t / P_0 = P(T > t) = s(t)$ 是活存機率（ Survival probability ），$P_t = P_0 s(t)$ ，瞬間死亡率的定義是

$$Z(t) = \lim_{\Delta t \to 0} \frac{P(t < T < t + \Delta t \mid T > t)}{\Delta t}$$

T 是年齡隨機變數

$$Z(t) = \lim_{\Delta t \to 0} \frac{P(T > t + \Delta t) - P(T > t)}{\Delta t \cdot P(T > t)} = \lim_{\Delta t \to 0} \frac{s(t + \Delta t) - s(t)}{\Delta t \cdot s(t)}$$

$$= -\frac{ds(t)}{dt} \frac{1}{s(t)} = -\frac{d \log s(t)}{dt} = -\frac{d \log [P_0 s(t)]}{dt}$$

$$= -\frac{d \log P_t}{dt}$$

$$\therefore \quad s(t) = e^{-\int_0^t Z(u) du}$$

$$s(t) = e^{-\alpha t} \qquad \text{if} \qquad Z(t) = \alpha$$

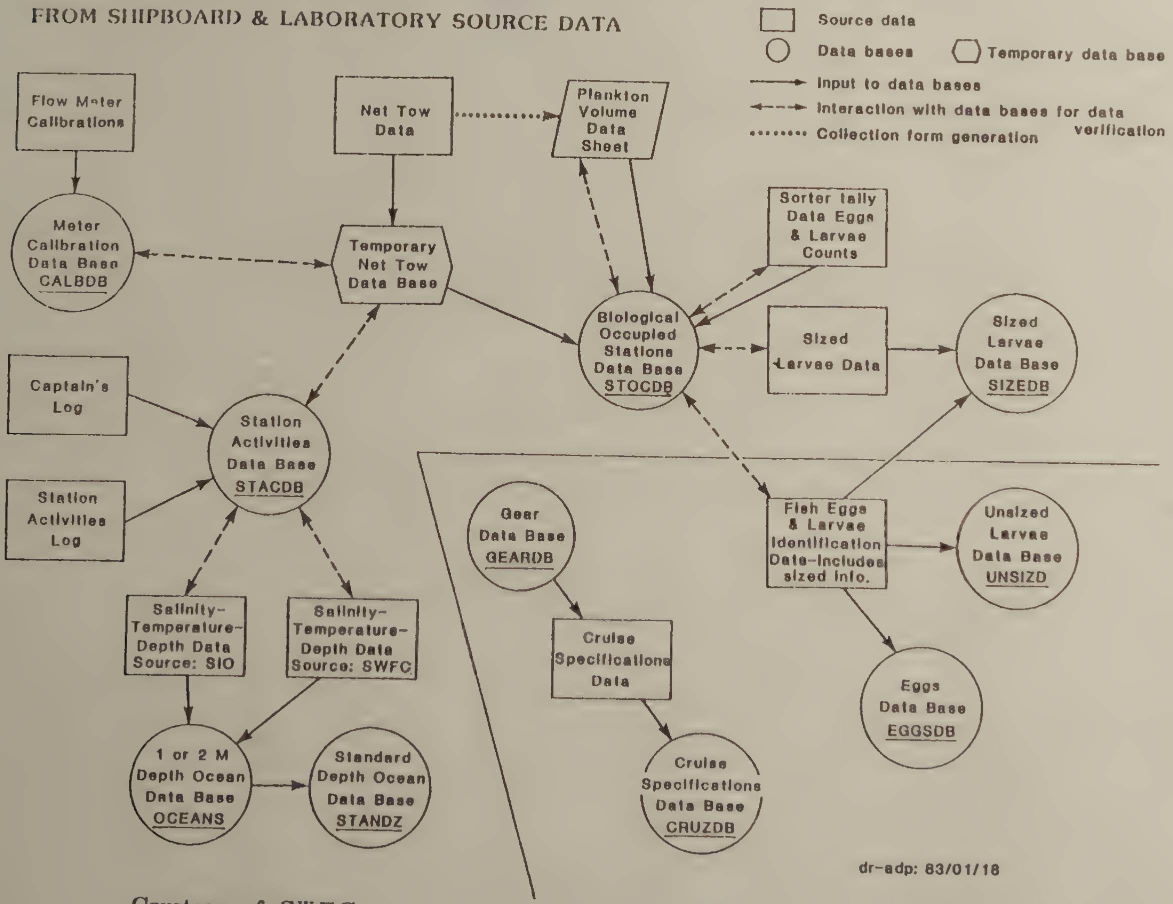
$$P_t = P_0 s(t) = P_0 e^{-\alpha t}$$

根據 1979－81 海洋調查所得魚卵資料，我們將鯷魚魚卵年齡頻度表列如下（ Lo 1985 ）

年齡間隔	平均年齡	平 均 值 P_t		
小時	t 日	1979	1980	1981
4－16	0.42	10.79	9.34	5.64
16－28	0.92	4.36	9.22	7.66
28－40	1.42	4.91	6.34	4.87

圖 7-3

FLOW DIAGRAM OF DATA BASE FILES CREATED
FROM SHIPBOARD & LABORATORY SOURCE DATA


Source data
Data bases
Temporary data base
Input to data bases
Interaction with data bases for data verification
Collection form generation
Flow Meter Calibrations
Meter Calibration Data Base CALBDB
Net Tow Data
Temporary Net Tow Data Base
Plankton Volume Data Sheet
Sorter tally Data Eggs & Larvae Counts
Biological Occupied Stations Data Base STOCDB
Sized Larvae Data
Sized Larvae Data Base SIZEDB
Captain's Log
Station Activities Log
Station Activities Data Base STACDB
Salinity-Temperature-Depth Data Source: SIO
Salinity-Temperature-Depth Data Source: SWFC
1 or 2 M Depth Ocean Data Base OCEANS
Standard Depth Ocean Data Base STANDZ
Gear Data Base GEARDB
Cruise Specifications Data
Cruise Specifications Data Base CRUZDB
Fish Eggs & Larvae Identification Data-Includes sized info.
Unsized Larvae Data Base UNSIZD
Eggs Data Base EGGSDB
dr-adp: 83/01/18

Courtesy of SWFC.

40－52	1.92	4.58	4.71	6.05
52－64	2.42	6.87	5.14	4.85
64－76	2.92	3.63		
$\hat{P}_0$ (SE)		9.76(2.82)	11.46(1.27)	6.73(1.32)
$\hat{\alpha}$ (SE)		0.33(0.28)	0.38(0.09)	0.11(0.13)

A、如何決定 $s(t)$ 或 $Z(t)$

a、繪圖（ P_t , t ），（ $\log P_t$, t ）或者（ $\log P_t$, $\log t$ ），直接由圖來決定 P_t 和 t 的關係。此法容易使用，但有時不精確（圖 7.4 ）（ Lo，1985 ）。

b、先推算 $Z(t)$，再由公式 $s(t)=e^{-\int_0^t Z(u)du}$ 計算 $s(t)$ 和 $P_t=P_0\, s(t)$。

$$Z(t)\approx\frac{[P_t-P_{t+\Delta t}]}{[\Delta t]\cdot P_t}$$ （表 7.1 ）（ Table 2 , Lo 1985 ）

根據鯷魚魚卵資料，我們獲得 $Z(t_i)=0.40$, 0.36 , 0.37 ，$\overline{Z(t)}=0.38$ ，所以 $Z(t)$ 是一常數，不隨年齡而變，$S(t)=e^{-\alpha t}$ ；$\alpha=\overline{Z(t)}$ 。

B、應用平均值或原有資料推算死亡率（看前頁）

在每年調查中，均設有一個魚卵資料檔案（ Data file ）具有年齡和觀察魚卵頻度（ Frequency ），平均每一記錄（ Record ）包括 A , B , C day old 魚卵和它們的年齡（表 6.3 ）。

	－A－		－B－		－C－	
Tow no.	t	P_t	t	P_t	t	P_t
1	×	×	×	×	×	×
2	×	×	×	×	×	×
3	×	×	×	×	×	×

另一魚卵檔案（ Data file ）經重新排列包括下列項目（表 6.4 ）

Tow no.	t	P_t
1	×	×
1	×	×
1	×	×
2	×	×
2	×	×
2	×	×

爲了推算瞬間死亡率 $Z(t)=\alpha$，我們可以直接將所有的（ t , P_t ）用來推算死亡率，因此我們有兩種資料:（ $\overline{t}$, $\overline{P}_{(t)}$ ）和（ t , P_t ），前者是將魚卵捕獲量分別按其年齡歸併於各年齡組（ 4－28h ），（ 28－40h ），（ 40－52h ），（ 52－64h ），（ 64－72h ），再計算每一小組的平均年齡（$\overline{t}$），和平均生產量（$\overline{P_t}$），後者是用原有資料來推算 $Z(t)$ ，一般

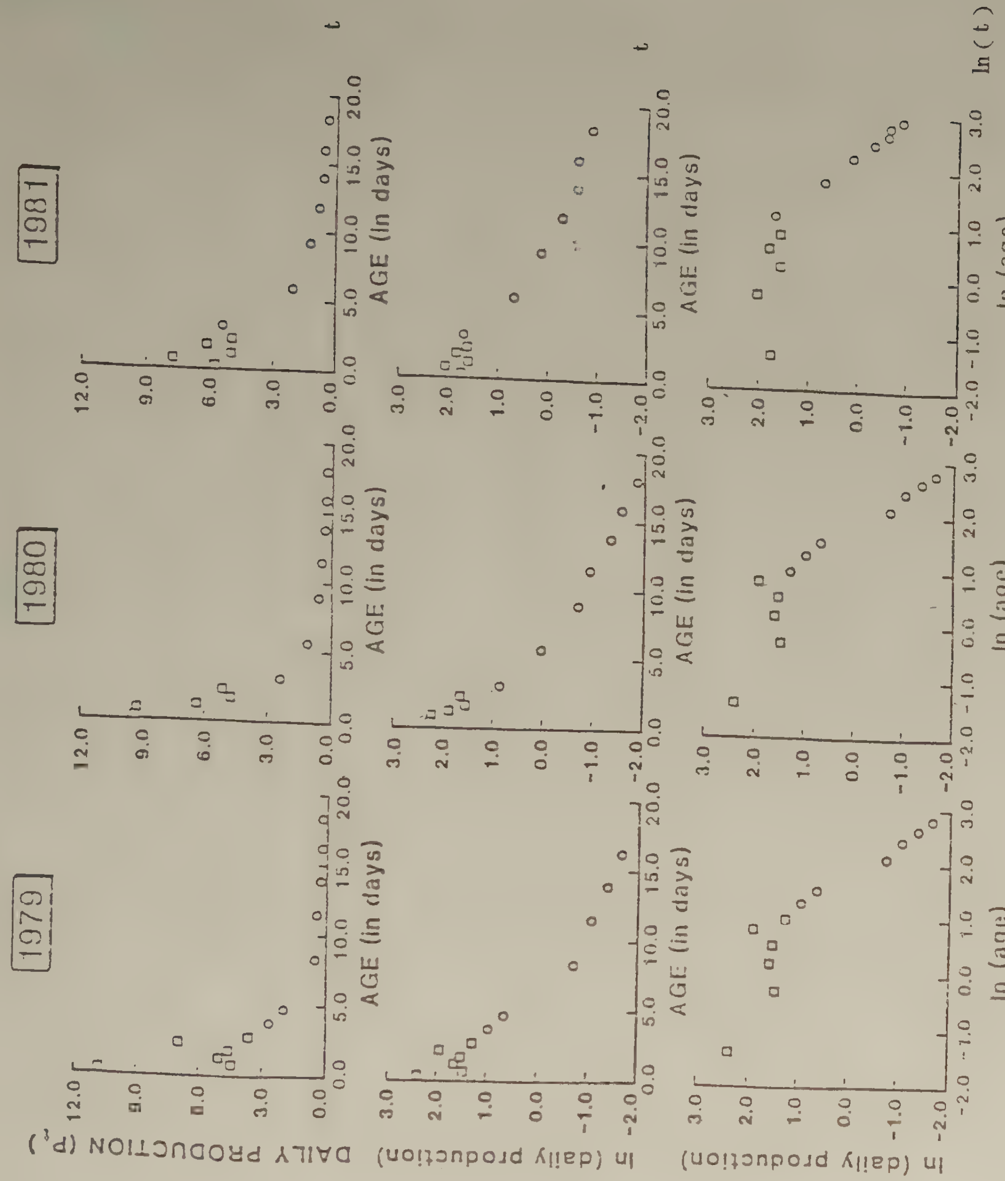


圖 7.4 Daily egg and larval production of Northern Anchovy per $0.05\,m^2$ (P_t) by age in days (t) and their log transformation ($\ln(P_t)$), 1979 — 1981.

A linear relationship between $\ln(P_t)$ and t indicates a constant instantaneous mortality rate (IMR) and a curvilinear relationship between $\ln(P_t)$ and t indicates an age dependent IMR. Squares are egg data and open circles are larval data.

表 7.1

The instantaneous mortality rates of anchovy eggs and larvae < 20 days ($z(t_i)$) by age in days ($\bar{t}_i$) computed from the daily egg and larval production estimates (P_{t_i}) and age (t_i), 1980.

i	t_i (days)	Daily egg and larval production P_{t_i}	$P_{t_{i-1}}-P_{t_i}$	t_i-t_{i-1}	$\bar{t}_i = (t_i+t_{i-1}/2)$	$z(t_i)^1$
1	0.67	9.28				
2	1.67	5.53	3.75	1.00	1.17	0.40
3	2.60	3.70	1.83	0.93	2.14	0.36
4	3.57	2.37	1.33	0.97	3.09	0.37
5	5.65	1.04	2.28	2.08	4.61	0.46
6	5.91	0.99	0.05	0.26	5.78	0.18
7	7.69	0.86	0.13	1.78	6.80	0.07
8	8.90	0.49	0.37	1.21	8.30	0.36
9	11.47	0.39	0.10	2.57	10.19	0.08
10	13.83	0.26	0.13	2.36	12.65	0.14
11	15.91	0.21	0.05	2.08	14.87	0.09
12	17.99	0.15	0.06	2.08	16.95	0.14

$z(t) = 0.0060 + 1.63/t$ is the function fitted to the data in the last two columns for $t > 4.5$ days.

[1] $z(t_i) = (P_{t_{i-1}}-P_{t_i}) / (t_i - t_{i-1}) / P_{t_i}$

而言兩種方法的結果差異甚小。

C、如果在 $P_t = P_0 s(t)$ 兩邊取了對數，而使公式線性化，即 $\ln P_t = \ln P_0 + \ln s(t)$ ，則迴歸最小平方法可以用來推算 Z(t)。但如果 P_0 是一項重要的參數，則非線性迴歸方法比較適合（ Lo 1986 ）。

7.3 仔魚（＜20 日，＜10 mm ）之死亡推算

仔魚死亡率之推算是根據魚體長頻度之資料，而非自一族資料（ Cohort data ）。我們的假設在平衡狀況（ Steady state ）下利用從海中捕獲之仔魚體長頻度分配（ Frequency distribution ），來推算一族狀況。但是魚網所捕獲之漁獲量是偏差的，因爲小魚會從魚網中漏出去，大魚會躲避魚網，若不考慮這些因素，則死亡率推算將是偏差的。對鯷魚之仔魚研究，美國西南漁業中心收集資料已有卅多年的歷史，爲獲得不偏差之死亡率推算，該中心先後做了幾個海上試驗（ Sea survey ）以計算各種網目之魚卵和仔魚的擠出率（ Extrusion rate ），並計算白晝／夜晚漁獲量比率來推算仔魚的躲避率（ Avoidance rate ）。在“仔魚死亡推算”前題下，我們將討論：1.仔魚因網目大小之留存率（ Retention rate due to mesh size ）與躲避魚網之留存率（ Retention rate due to avoidance ）2.仔魚生產率（ production rate ）之推算和各種修正因素之公式，3.死亡率的模式。

A、仔魚在魚網中之留存率（ Retention rate ）

a、仔魚之擠出率（ Extrunsion rate ）和留存率（ Retention rate ），（擠出率＝1－留存率）：在過去卅年中西南中心曾用不同的魚網捕獲仔魚。

年 度	網 架	網 目	網地質料
1951－68	1m ring net	.55 mm	Silk 絲
69－77	〃	.505 mm	Nitex 尼龍
78－Now	Bongo	.505 mm	〃
80－82	Calvet	.333 mm	〃
83－Now	〃	.150 mm	〃

爲了計算各種網目之仔魚擠出率，我們先後進行四種網目試驗。

年 度	大網目	小網目	試 驗
1966－68	1m silk net of .55 mm	1/2 m Nylon net of 0.333 mm	(1)
1969	monofilament .505 mm	〃	(2)

1982	.333 mm	.150 .075 mm	(3)
1983	Nitex .505 mm	.333 mm	(4)

資料來自試驗(1)和試驗(3)用來估計 0.55 mm 仔魚擠出率。

試驗(4)和試驗(3)用來估計 .505 mm 擠出率，試驗(3)用來估計 .333 mm 擠出率。

a1. 1982 網目試驗（Lo 1983）

1982 年三月，我們在洛山磯灣裏選擇了 Anchovy 區的一個測站，作了爲期一週的海上試驗。一共有 142 拖網次，每一個網次包括繫在一起的三種魚網，其網目爲 .333，.150 和 0.075 mm，這些魚網垂直投放在 70 m 的深度再垂直收回。魚卵和仔魚體長頻度均用來推算它們的擠出率，這些擠出率和其它試驗所得之擠出率（比較 .505 mm 與 .333 mm 之漁獲量）合併起來推算大網目之魚卵和仔魚的衝出量。

在此試驗中，三個魚網之位置，在每六小時內兩個魚網互換位置，避免位置所引起的漁獲量之偏差。

欲檢查三種網目之平均漁獲量不一樣的假設，魚卵與小於 4.5 mm 仔魚歸於一項檢定——多變數變方分析（Multivariate analysis of variance ; MANOVA）。大於 4.5 mm 的仔魚則用 χ^2 檢定，因爲後者有 0.69－0.97 的樣本，其漁獲量爲零。（仔魚分類成 2.0，2.5，3.0， 6.0，6.5^+ mm）。

在多變數變方分析中，每一樣本單位（Sampling unit）的觀察量是魚卵，2.0，2.5，……，4.0 mm 之漁獲量。因爲有些仔魚頻度分配是偏斜的（Skew），所以先應用對數變換 $x = \ln(y+1)$ 再行分析。

首先使用雙向（Two way）MANOVA；一方是網目（0.075，0.150 和 0.333 mm），一方是網所在位置〔右方（Starboard），中間，和左方（Port）〕，結果是位置對漁獲量並無顯著的影響（Significant effect），但是網目對漁獲量有顯著的影響。因爲魚網位置無關緊要，我們就使用單向 MANOVA；0.075 mm 和 0.150 mm 合併的漁獲量平均值與 0.333 mm 網目之漁獲量之平均值比較，其差別是顯著的，至於比較 0.075 和 0.150 mm 網目除了魚卵外，仔魚平均值的差異不大。結論是一部分的魚卵和小於 4.5 mm 的仔魚自 0.333 mm 網目漏出。

至於比較在三個網目下之大於 4.5 mm 的仔魚擠出率，我們用了 χ^2 測驗。對於每一體長之仔魚，我們作一個 2×3 的列聯表（Contingency table），一邊是三種網目，一邊是無仔魚和有仔魚的樣本次數，所以一共有 5 個 χ^2 Value。除了最大體長之仔魚組的結果是明顯不同外，其它 χ^2 數值都甚小。因爲組間（Among groups）沒有什麼相關，

五個 χ^2 數可以加起來檢定“有仔魚”和“無仔魚”之分配是否與網目大小有關，結果是 χ^2 統計值（11.94）在5％之顯著水準下甚小（表7.2；Lo 1983）。

a2. 仔魚和魚卵之留存率推算

目前每年之海上調查是用Bongo 0.505 mm和Calvet 0.150 mm之漁網。Bongo 0.505 mm的留存率是根據1982年和1983年兩次海上試驗所得的結果。

以下是仔魚和魚卵自不同網目之留存率推算值：

仔魚：網目　　　留存率是魚體長之函數（R_L）

0.505 mm

$$R_L = \begin{cases} \{1+e^{4.38-1.066L}\}^{-1} & L < 6.5\ \text{mm} \\ 1 & L \geqslant 6.5\ \text{mm} \end{cases}$$

0.555 mm

$$R_L = \begin{cases} \{1+e^{4.58-1.098L}\}^{-1} & L < 6.5\ \text{mm} \\ 1 & L \geqslant 6.5\ \text{mm} \end{cases}$$

0.333 mm

$$R_L = \begin{cases} 0.63 & L < 4.25\ \text{mm} \\ 1 & L \geqslant 4.25\ \text{mm} \end{cases}$$

L：魚體長（*mm*）

魚卵：網目	留存率
0.505 mm	0.29
0.55 mm	0.27
0.333 mm	0.91

b、仔魚因躲避魚網（Avoidance）之留存率（Hewitt and Methot 1982）

仔魚隨年齡之增長逐漸會躲避魚網。其躲避的程度與仔魚體長和光線之強弱有關。雖然我們沒有仔魚躲避魚網之直接觀測值，但爲了要推算因其躲避魚網之仔魚的留存率，我們比較白晝（0830 — 1630）與夜晚（2030 — 0230）的漁獲量，並按體長推算出漁獲量的比率：

用 DN_L 來代表魚體長 L_{mm}（Live size）中午（1200小時）和午夜（2400小時）漁獲量之比率

$$DN_L = 2.4931 \times \text{Exp}(-0.2304 \times L)$$

留存率（f）則因體長（L）和時間（t）而異：

$$f = \frac{1+DN_L}{2} + \frac{1-DN_L}{2}\left[\cos\left(2\pi\frac{t}{24}\right)\right]$$

B、各年齡之仔魚生產量（Larval production）

因爲魚網所導致之漁獲量偏差，我們必須按魚體長，調整觀測之頻度，在此有三種

表 7.2 Number of samples with zero catch from a total of 140[1] samples for anchovy eggs and larvae by length group, the maximum catch for each of three mesh sizes and the chi-square values for larvae ≥ 4.5mm based upon three-vertical-net-experiment, 1982.

	Number of samples with zero catch			Maximum catch			chi-square d.f.=2
	0.075mm	0.150mm	0.333mm	0.75mm	0.150mm	0.333mm	
Eggs	0	0	0				
2.0 mm	42	38	33				
2.5	16	10	9				
3.0	0	0	2				
3.5	7	8	18				
4.0	27	24	52				
4.5	103	97	97	8	3	5	0.83
5.0	111	107	103	5	3	5	1.27
5.5	131	133	136	2	1	1	2.0
6.0	132	130	133	2	1	1	0.6
6.5+	117	102	118	2	3	2	7.24*
							11.94 (d.f.=10)

[1] Two samples were discarded because they were spoiled.

*Significant at 5% level.

變數須要考慮。a、因體長而異之網擠出率。b、因體長而異之躲避率。c、網中海水滲透之總體積。除此以外，爲了計算死亡率，我們必須將體長變換成年齡，每一體長間隔（ Length category ）之頻度受成長率快慢之影響，成長率慢的在此一體長間隔的持續時間（ Duration ）就長，在樣本中觀測之頻度（ Frequency ）就顯然地高，因此我們必須計算每單位時間生產量〔 Production per time unit （日或小時…）〕有如物理之流率（ Flux ）。如此對於觀測之頻度共有四種加權（ Weight ）。

仔魚自海中捕獲後，均分類成 1 mm 的項目：2.5 mm（包括 2.0，2.5，3.0 mm），3.75 mm（ 3.5，4.0 mm ），4.75 mm（ 4.5，5.0 mm ）………每一體長之頻度分配均由負二項分配來配合（ Fit ），並考慮到各種偏差因素。Bessel（ 1972 ）提出一加權負二項分配模式，本中心兩位同仁即應用此模式來推算各體長之平均生產量（ Zweifel and Smith 1981 ）。

加權負二項分配的密度函數爲：

$$f(x_i \mid w_i) = \left(\frac{k}{mw_i + k}\right)^k \left(\frac{mw_i}{mw_i + k}\right)^{x_i} \frac{(k + x_i - 1)!}{x_i!\,(k-1)!}$$

$$\text{Likelihood function} = \prod_{i=1}^{n} f(x_i \mid w_i)$$

Where w_i ＝四項修正因素之乘積＝ $w_{1i} \cdot w_{2i} \cdot \cdots\cdots \cdot w_{4i}$

w_{1i} ＝因擠出魚網之留存率

w_{2i} ＝因躲避魚網之留存率

w_{3i} ＝仔魚在一體長間隔（ Length category ）之持續時間（ duration ）

w_{4i} ＝魚網滲水體積／某一單位滲水體積

n＝拖網總數

$$E\,x_i = mw_i \qquad \mathrm{Var}(x_i) = m_i + \frac{m_i^2}{k} = m_i\left(1 + \frac{m_i}{k}\right)$$

m_i 是母體平均值

m 是在無擠出、無躲避，仔魚每一單位滲水體積之平均單位時間之漁獲量（ Production per unit time ）。

由每一體長之仔魚，我們可推算 m_t（$\hat{m}_t$），（$\hat{m}_t$，t）即用於推算仔魚之死亡率。（表 7.3 Zweifel and Smith 1981 ）。

C、隨年齡而變之仔魚死亡率（ P.142－144, Lo 1985 ）

表 7.3

(1) Estimates of live[a] size at age of anchovies for the classes of preserved larvae[b] regularly taken during CalCOFI surveys and the estimated "effective sampler size" w for a standard volume of water strained during a tow at time of maximum catch (2300 h).

Group	Preserved size	Recorded size	Live size Begin	Live size End	Average size	Age from hatch	Days in interval	Weight factor[c] "w" 13°	16.2°	19°
0	0.0– 0.5	0.00	0.02	2.52	0.72	−1.31	2.47	0.60	0.37	0.27
1	2.0– 3.0	2.50	2.52	3.94	3.23	0.67	1.95	0.63	0.39	0.28
2	3.5– 4.0	3.75	3.94	5.04	4.49	5.14	4.69	2.11	1.30	0.93
3	4.5– 5.0	4.75	5.04	6.10	5.57	8.01	2.67	1.59	0.98	0.71
4	5.5– 6.0	5.75	6.10	7.15	6.62	10.53	2.40	1.73	1.07	0.77
5	6.5– 7.0	6.75	7.15	8.17	7.66	12.83	2.21	1.79	1.10	0.79
6	7.5– 8.0	7.75	8.17	9.18	8.68	14.96	2.07	1.68	1.04	0.74
7	8.5– 9.0	8.75	9.18	10.19	9.68	16.98	1.97	1.60	0.99	0.71
8	9.5–10.0	9.75	10.19	11.19	10.69	18.91	1.90	1.54	0.95	0.68
9	10.5–11.0	10.75	11.19	12.18	11.69	20.78	1.85	1.49	0.92	0.66
10	11.5–12.0	11.75	12.18	13.18	12.68	22.61	1.81	1.46	0.90	0.65
11	12.5–13.0	12.75	13.18	14.18	13.68	24.40	1.78	1.44	0.89	0.64
12	13.5–14.0	13.75	14.18	15.17	14.68	26.17	1.76	1.43	0.88	0.63
13	14.5–15.0	14.75	15.17	16.17	15.67	27.93	1.76	1.42	0.88	0.63
14	15.5–16.0	15.75	16.17	17.15	16.66	29.66	1.71	1.38	0.86	0.61
15	16.5–18.0	17.25	17.15	19.16	18.15	32.29	3.55	2.87	1.77	1.27
16	18.5–20.0	19.25	19.16	21.18	20.17	35.87	3.62	2.93	1.81	1.30
17	20.5–22.0	21.25	21.18	23.21	22.19	39.55	3.75	3.03	1.87	1.34
18	22.5–24.0	23.25	23.21	25.24	24.22	43.38	3.93	3.18	1.96	1.41

[a] Shrinkage corrections are based on the work of Theilacker (1980).

[b] Zweifel and Lasker (1976) assign a development equivalent length to eggs (Group 0) in order to utilize the same equation for development and growth.

[c] At 2300 h and 3.5 m^3 water strained per meter of depth.

(2) Number of 3.75 size class larvae taken in January, February and March of 1969 in southern California inshore Region 7 by station with hour, temperature at 10 m depth and standard haul factor = 10/volume strained/depth. Stations are identified in Kramer et al. (1972).

	January				February			
Station	Hour	Temp	SHF	Larvae	Hour	Temp	SHF	Larvae
80.51	17.98	13.06	2.99	9	05.03	13.22	3.41	69
.52	19.88	13.02	3.15	3	03.20	13.29	3.48	28
.55	22.23	13.22	3.42	21	00.10	12.85	3.82	1
.60	12.82	12.82	3.29	0	20.18	12.84	4.36	0
82.47	14.70	14.07	3.15	84				
83.40	08.95	14.31	.73	291	06.67	13.51	1.89	51
.43	11.55	14.43	3.22	343	10.12	12.90	3.67	18
.51	04.35	13.46	2.95	45	19.35	12.58	3.97	1
.55	01.35	13.29	3.26	0	22.43	13.17	3.29	4
87.33	21.93	14.20	2.35	115	17.25	14.20	2.60	103
.35	00.38	14.76	3.44	149	20.12	13.87	2.99	244
.40	03.12	14.03	3.25	550	21.78	13.89	3.44	88
.45	05.78	14.26	3.02	311	00.68	14.07	3.34	114
.50	08.22	13.44	2.95	14	03.18	12.80	2.93	10
.55	10.47	14.31	3.29	7	05.87	13.31	3.41	191
90.28	12.28	14.49	3.36	144	00.78	14.33	3.34	390
.32	09.05	14.79	3.29	223	22.18	14.63	3.17	1 012
.37	06.28	14.96	3.37	370	18.97	14.86	3.24	275
.39					15.68	14.80	3.48	243
.45	01.07	13.44	3.35	35	12.10	13.93	3.23	195
.53	20.77	14.68	3.30	632	09.37	13.80	3.20	84
93.27	09.93	14.03	2.89	21	05.32	14.36	2.72	820
.28	11.98	14.12	3.34	2	06.78	14.38	3.05	287
.30	14.07	14.05	3.25	4	09.37	14.45	3.45	1 343
.35	17.12	15.52	3.18	2	15.40	14.45	3.02	843
.40	19.93	14.31	3.20	118	20.28	14.78	3.19	115
.45	22.88	15.42	3.12	2	23.10	13.96	3.11	254
.50	01.72	15.56	3.39	0	01.68	14.65	3.14	385
94.30	07.37	14.31	2.97	46	17.03	13.91	3.29	354
97.29	12.57	14.88	2.04	44	09.10	14.22	2.60	120
.30	13.85	15.02	2.82	7	08.52	14.18	2.53	77
.32	17.28	15.08	2.81	18	07.53	14.35	3.14	79
.35	20.52	15.04	2.59	0	04.20	14.35	3.13	34
.40	01.10	15.48	3.00	0	01.40	14.20	3.18	117
		March						
90.45	09.10	13.72	3.31	282				

表 7.3（續）

---

(3) Abundance classes of 3.75 mm larvae taken in the first quarter of 1969 in the southern California inshore Region 7 with average effective sampler size,[a] age at 16.2° C, and corrections for bias due to temperature, volume of water strained, avoidance and extrusion.

Lower–Mark–Upper	No. of stations	Weight[a]	Age[b]	Temp[c]	Vol.[d]	Avoid[e]	Escape[f]
0	6	1.28	7.02	3.20	.88	.73	.63
1	2	1.04	8.75	3.99	.73	.56	.63
2	3	.85	6.10	2.78	.89	.54	.63
3	1	1.10	8.30	3.78	.91	.51	.63
4	2	1.53	7.55	3.44	.87	.80	.63
7	2	.96	6.40	2.92	.94	.56	.63
9	1	1.06	8.24	3.76	.95	.47	.63
10	1	1.79	8.62	3.93	.97	.74	.63
14	1	.75	7.73	3.53	.97	.35	.63
16– 21–32	5	1.21	7.49	3.42	.89	.64	.63
33– 43–64	6	1.63	7.12	3.24	1.10	.74	.63
65– 99–128	13	1.21	6.96	3.17	.94	.65	.63
129–205–256	8	.93	6.84	3.12	.87	.54	.63
257–329–512	10	1.28	6.68	3.04	1.19	.58	.63
513–771–1024	5	1.55	6.62	3.02	.93	.88	.63
1025–343–2048	1	.80	6.59	3.01	.83	.51	.63

[a] Average product of individual weighting components.

[b] Calculated from equations obtained from laboratory growth experiments. Temperature Specific Equations for growth and development of anchovy, *Engraulis mordax*, during embryonic and larval stages.

[c] Calculated as estimated time in size interval/standard time = 2 days.

[d] Calculated as estimated volume of water strained/standard volume = 3.5 m^3 per meter depth.

[e] Calculated as long term catch by hour/standard or maximum catch at 2300 h.

[f] Determined from mesh retention study of Lenarz (1972).

自 1980 年仔魚資料（表 7.4 ； Lo 1985）我們擬定的仔魚瞬間死亡率是隨年齡而變的： $Z(t)=\beta/t$ 。首先計算樣本瞬間死亡率 $Z(t_i)=(P_{t_{i-1}}-P_{t_i})/(t_i-t_{i-1})/P_{t_i}$ 以略估在年齡 t_i 時的 $\frac{ds(t)}{dt}\cdot\frac{1}{s(t)}=Z(t)$（表 7.1）。$Z(t)$ 和 t 之間的關係決定 $Z(t)$ 之方程式形式。魚卵和小於 4.5 日之仔魚的 $Z(t)$'S 是近於一常數，但是大於 4.5 日的仔魚，其 $Z(t)$ 是隨年齡（t）而減小，$Z(t)=\beta/t$ 被認爲是描述仔魚死亡率的最佳模式，所以仔魚（＜20 日）的 Conditional 留存機率

$$s(t)=e^{-\int_{t_c}^{t}Z(u)du}=\left(\frac{t}{t_c}\right)^{-\beta} \qquad t_c<t<20\text{ 日}$$

與魚卵死亡率合併則得

$$s(t)=\begin{cases} e^{-\alpha t} & t\leqslant t_c \\ e^{-\alpha t_c}\left(\frac{t}{t_c}\right)^{-\beta} & t_c<t<20\text{ 日} \end{cases}$$

仔魚死亡曲線

$$P_t=P_0e^{-\alpha t_c}\left(\frac{t}{t_c}\right)^{-\beta}=P_{t_c}\left(\frac{t}{t_c}\right)^{-\beta} \qquad (7.1)$$

t_c 或是孵化年齡（～2.5 日），或是卵黃囊年齡（4.5 日）。

在西南中心，我們已有現成的電腦軟體用來計算仔魚生產率（Larval production rate）詳細程序，請直接向編者函索。

生產量和年齡（P_t, t）之資料（$t<20$ 日）透過電腦之 STATISTICAL PACKAGE 的 Nonlinear regression 則可獲得 $\hat{P}_{t_c}$ 和死亡率係數 $\hat{\beta}$ （圖 7.4 ； Lo 1985）。

表 7.4

Daily egg and larval production per 0.05 m^2 (P_t) at various ages in days (t) sampled from CalVET and Bongo tows, and the estimates of five parameters: egg production at age zero ($\hat{P}_0$), egg mortality ($\hat{\alpha}$), larval mortality coefficient ($\hat{\beta}$), larval production at hatching ($\hat{P}_I$) and incubation time in days (t_I) in CalCOFI regions 4, 7, 8, and 11, Jan-Apr, 1979-81.

	1979[1]			1980		1981			
	t	P_t	Live standard length (mm)	t	P_t	t	P_t	Live[3] standard length (mm)	
Eggs	0.4167	10.79		0.4167	9.34	0.4167	5.64		
	0.9167	4.36		0.9167	9.22	0.9167	7.66		
	1.4167	4.91		1.4167	6.34	1.4167	4.87		
	1.9167	4.58		1.9167	4.71	1.9167	6.05		
	2.4167	6.87		2.4167	5.14	2.4167	4.84		
	2.9167	3.63							
Larvae	3.73	2.64	3.03	2.94	2.26	3.14	3.23	3.03	CalVET net
				4.08	2.39	4.35	2.99	3.59	
				5.91	0.99	6.25	2.10	4.13	
				7.69	0.86	8.08	1.84	4.66	
	4.72	1.96	3.26	3.05	2.35	3.10	5.29	2.97	Bongo net
	8.32	0.48	4.17	5.65	1.04	5.86	1.96	4.00	
	11.49	0.35	5.69	8.90	0.49	9.22	1.10	5.13	
	13.90	0.25	6.77	11.47	0.39	11.79	0.72	6.23	
	16.24	0.19	7.83	13.83	0.26	14.01	0.54	7.30	
	18.31	0.13	8.87	15.91	0.21	16.01	0.53	8.35	
				17.99	0.15	18.22	0.41	9.38	
$\hat{P}_c$		9.76	[2](2.82)	11.46	(1.27)	6.73	(1.32)		
$\hat{\alpha}$		0.33	(0.28)	0.38	(0.09)	0.11	(0.13)		
$\hat{\beta}$		1.83	(0.14)	1.24	(0.17)	1.19	(0.17)		
$\hat{P}_I$		3.59	(0.18)	2.51	(0.19)	4.81	(0.42)		
t_I		3.21		2.96		2.85			

---

[1] Not weighted by area size.

[2] Asymptotic standard error in ( ).

[3] For both 1980 and 1981 larval data.

PRESERVED SIZE (mm)	LIVE SIZE (mm)	(t) AVE. AGE (day)	($_wP_t$) DAILY LARVAL PROD./0.05 m^2
2.50	3.26	4.91	0.518
3.75	4.57	8.60	0.121
4.75	5.69	11.58	0.0838
5.75	6.27	14.15	0.0665
6.75	7.83	16.41	0.0481
7.75	8.87	18.62	0.036

$$_wP_t = 1.364\ (t/3.16)^{-2.217}$$

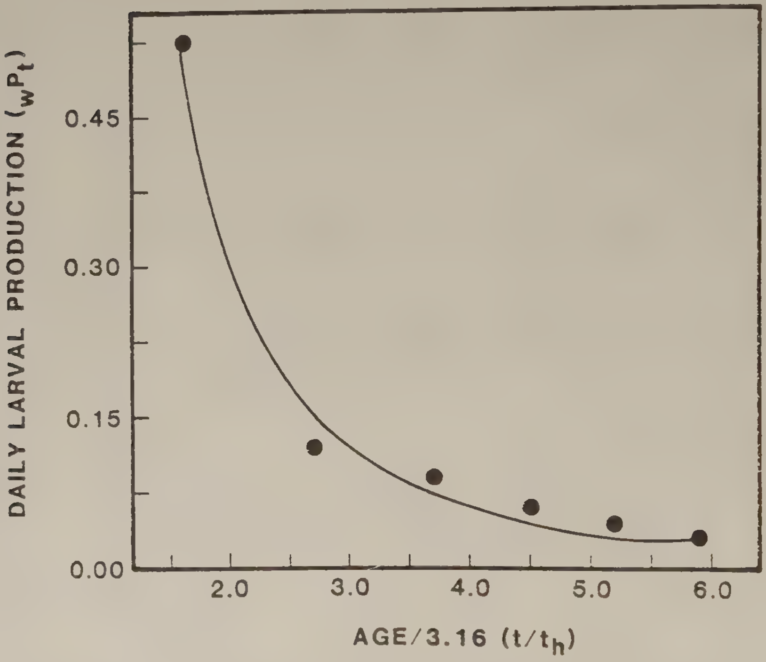


圖 7.5 DAILY LARVAL PRODUCTION PER 0.05 m^2 ($_wP_t$) AT AGE t, 1979

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The California Current System: The Seasonal Variability of its Physical Characteristics

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The seasonal variation of the physical characteristics and of large-scale current patterns of the California Current system is examined using harmonic analysis applied to the 23 years of California Cooperative Oceanic Fisheries Investigations data collected between 1950 and 1978. The amplitude and phasing of seasonal variation in dynamic height and the overall standard deviation of dynamic height define three domains: oceanic, coastal, and an intervening transition zone. The transition zone is a broad band centered approximately 200–300 km offshore and parallel to the coast in which the seasonal range of dynamic height is a relative minimum and the standard deviation is a maximum. It is hypothesized that recurrent mesoscale eddies and energetic meanders create this zone. Such eddies and meanders would contribute heavily to the standard deviation of dynamic height but not its seasonal variation. The transition zone is coincident with the core of flow of the California Current. A strong interaction between the core of the California Current and the mesoscale eddy field is evident. Seasonal variation in the fields of temperature, salinity, σ_t, and oxygen is related to variations in the California Current, the Inshore Countercurrent and the California Undercurrent through vertical adjustments in the density field and through changes in transport. In the undercurrent there is an especially strong relation between seasonal variations in strength of flow and the extreme values of water mass characteristics.

1. INTRODUCTION

The California Current (CC) is the eastern limb of the large-scale, anticyclonic North Pacific gyre. Except near the coast, the CC is a surface (0–300 m deep) current which carries water equatorward throughout the year along the west coast of North America to the North Equatorial Current. The average speed of the CC off the coast of California is typically less than $25\ \mathrm{cm\ s^{-1}}$ [*Reid and Schwartzlose*, 1962]. Daily average surface speeds, as high as $50\ \mathrm{cm\ s^{-1}}$, have been observed using drifters [*Davis*, 1985]. The characteristics of the CC (i.e., low temperature, low salinity, high dissolved oxygen) change abruptly to the west, at the California Front [e.g., *Saur*, 1980]. Here, a region of complex salinity structure, a southeastward continuation of the Subarctic Frontal Zone, lies between the CC and the waters typical of the eastern North Pacific water mass [e.g., *Lynn*, 1986]. *Sverdrup et al.* [1942] use this water mass boundary as the western limit of the CC. It lies 850 to 900 km off the California coast. Near the coast (typically within 150 km), there is a seasonal change in the direction of this surface flow. Throughout the fall and winter, the direction of this narrow zone of coastal surface flow is often poleward [*Reid and Schwartzlose*, 1962; *Hickey*, 1979; *Chelton*, 1984]. We refer to this poleward flow as the Inshore Countercurrent (IC). North of Point Conception the IC is often referred to as the Davidson Current. There is inshore poleward flow along southern California and Baja California as well, and at times it is continuous about the headland at Point Conception [e.g., *Hickey*, 1979]. We prefer the general description "Inshore Countercurrent" rather than regional names for what may be a general phenomenon. (This choice is not meant to imply temporal and spatial continuity of flow.)

The California Undercurrent (CU) is considered to originate in the eastern equatorial Pacific and to flow poleward along the North American coast [*Sverdrup and Fleming*, 1941; *Reid et al.*, 1958]. *Reid* [1962, 1963], on the basis of drogue measurements, was the first to suggest that this flow might be concentrated in a relatively narrow high-speed core off both Point Conception and Baja California. *Wooster and Jones* [1970] further confirmed the existence of the high speed core off Baja California with hydrographic and direct current meter observations. *Hickey* [1979] reviewed the available observations of the CU from San Francisco to Baja California and concluded that the CU shows considerable seasonal variability in position, strength, and core depth. She relates aspects of the current field and seasonal variability to the fields of wind stress and curl of the wind stress. *Chelton* [1984] examined seasonal variability of the nearshore geostrophic velocity along California mostly limited to the region between Point Sur and Point Conception. His study attempts to relate the observation record to various models of ocean dynamics.

The water properties of these currents are determined by four water masses, each defined by its temperature, salinity, dissolved oxygen, and nutrients at the time it enters the California Current system. Pacific Subarctic water forms at high latitudes in regions of excess precipita-

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TABLE 1. Relative Comparison of Water Masses of the California Current and California Undercurrent [From *Simpson*, 1984*a*]

	T	S	O_2	Nutrients
Surface water masses (0–200 m)				
Pacific Subarctic	L	L	H	H
North Pacific Central	H	H	L	L
Coastal Upwelled	L	H	L	H
Subsurface water masses (200–500 m)				
Equatorial Pacific	H	H	L	H

L, low; H, high.

tion and heat loss. This water is entrained in the Subarctic Current and West Wind Drift, and it enters the CC near 48°N [*Pickard*, 1964]. It has relatively low temperature T, low salinity S, high dissolved oxygen O_2, and high phosphate [*Reid et al.*, 1958; *NORPAC Committee*, 1960, plates 9 and 14]. Water of Pacific Subarctic origin is still recognizable by its relatively low salinity as it leaves the CC near 25°N [*Reid et al.*, 1958]. Pacific Subarctic water gives the CC its offshore near-surface salinity minimum and high dissolved oxygen. Eastern North Pacific Central water [*Sverdrup et al.*, 1942; *Pickard*, 1964] is warm, salty, and relatively low in dissolved oxygen and nutrients [*Reid et al.*, 1958]. It enters the California Current system from the west. Equatorial Pacific water forms in the eastern tropical Pacific and has relatively high temperature, high salinity, high nutrients, and low dissolved oxygen [*Sverdrup et al.*, 1942; *Pickard*, 1964]. It enters the deeper-lying CU from the south. Upwelling within 50 km of the California coast brings relatively cold, salty, nutrient-rich, and oxygen-deficient water from depth to the surface [*Sverdrup*, 1938; *Reid et al.*, 1958]. A summary of these water properties is given in Table 1.

In this study we describe the seasonal variation of the physical characteristics and large-scale current patterns of the California Current system and their interrelationships. Although other authors have described and discussed aspects of the seasonal variation for some of its characteristics at some depth levels and for some subregions, we attempt to provide an integrated picture of the mean seasonal variation of the physical characteristics of the California Current system over the entire domain from the coast to approximately 1000 km offshore and from San Francisco to southern Baja California using data collected over the period 1950 through 1978.

2. DATA

Large-scale systematic hydrographic sampling of the California Current system was initiated in 1949 by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program. Since 1950, stations have been repeatedly occupied at varying intervals based on a geographically fixed grid. The station occupation record is given by *Eber and Wiley* [1982]. In all, over 16,000 stations have been occupied from 1950 through 1978. Those stations for which there is an accumulation of observations adequate for the determination of seasonal cycles fall in a region extending offshore to 700 km and from San Francisco to southern Baja California. The sampling grid is based on parallel lines oriented approximately perpendicular to the coast (Figure 1*a*). The separation of the lines

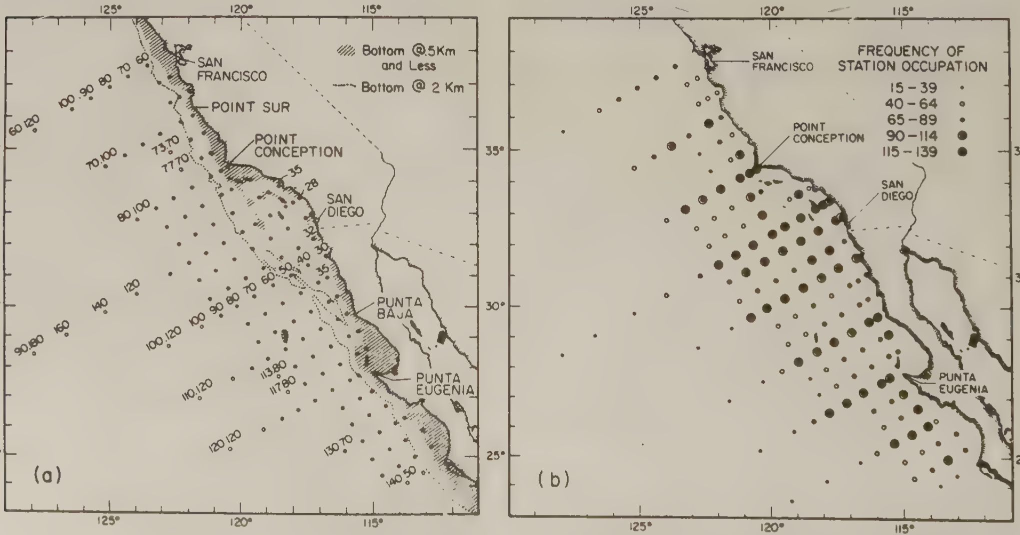

Fig. 1. (*a*) CalCOFI station pattern. Harmonic analysis was applied to data for all stations shown here. The 2000-m isobath is shown dotted. Bathymetry less than 500 m is hatched. (*b*) Record of station occupation.

and the standard spacing of stations are both 74 km. Near shore the station spacing is half or less, and at the western edge of the pattern it is sometimes double. The original grid spacing was designed upon units of nautical miles (1 n. mi = 1.852 km). Standard line/station spacing was 40 n. mi; one unit of station number equals 4 n. mi, and one unit of line number equals 12 n. mi. (In this strict notation, station lines such as 93 and 97 are actually 93.333... and 96.666... .)

Through 1964, 18-bottle Nansen casts were the standard sampling method at hydrographic stations. After 1964, salinity-temperature-depth (STD) and conductivity-temperature-depth (CTD) casts were taken alone, in conjunction with a Nansen cast, or with a few water bottle samples for calibration. In addition to measurements of temperature and salinity, determinations of oxygen concentration frequently were made. Values of the oceanographic measurements and computed parameters are interpolated to 14 standard levels (0, 10, 20, 30, 50, 75, 100, 125, 150, 200, 250, 300, 400, and 500 m).

In general, the minimum criterion for analysis of seasonal variation was a station occupancy of 40 or more (Figure 1*b*). In the heavily sampled areas near the coast and especially in the Southern California Bight, the occupancy requirement was set higher to avoid large differences between neighboring stations. Most stations near the western boundary of the CalCOFI grid have been occupied less than 40 times. Data for these latter stations may be insufficient to properly resolve seasonal variability. They are, however, included in this analysis because they provide the best available information, albeit limited, on seasonal cycles in the far offshore domain of the California Current system. The station lines numbered in whole decades (every third line in Figure 1*a*) are termed cardinal lines and generally have been occupied more frequently than the other lines. The cardinal lines were chosen for more detailed analysis in this study.

3. Methodology

We fitted harmonic curves composed of annual and semiannual components to each data record by regression analysis using the method of least squares. These curves provide an expression of the mean seasonal variation of each data record [*Lynn*, 1967; *Chelton*, 1982, 1984; *Godfrey and Ridgway*, 1985]. There are five data records at each grid point, one each for temperature, salinity, σ_t, dissolved oxygen, and dynamic height. There is a grid point for each of the 14 standard depths, at each selected station. Each harmonic curve is described by five coefficients. The coefficients are used to generate an estimate of a "mean" value of a characteristic at each standard level for any given time of the year. From these mean values we computed mean seasonal range of characteristics, days of occurrence of seasonal extremes, and mean seasonal differences between specified dates. We also computed the vertical distribution of isopleths of a characteristic versus time of year. It should be noted that a few of the figures given herein are derived from arithmetically averaged data where such maps would not differ from those produced by least squares fit to harmonics. They are noted in the captions as taken from *Lynn et al.* [1982].

Geostrophic velocities relative to 500 dbar were calculated from the station-to-station differences between the harmonic curves expressing dynamic height (see *Chelton* [1984] for a thorough analysis of the methodology). The choice of 500 dbar as the reference level is dictated by the data set. *Wyllie* [1966] shows the current field at 500 m relative to 1000 dbar to be very weak. At this level there is a relief of 1 to 2 dyn cm over the CalCOFI grid which gives an estimated flow of less than 1 cm s^{-1}. It is possible, however, that currents at 500 m may be more substantial in the vicinity of ridges and the continental slope. Geostrophic velocities are underestimated by the coarse station spacing in regions where flow consists of a narrow jet such as the CU [*Wooster and Jones*, 1970]. Hence we cannot derive the details of the narrow CU and IC flows. The spatial scale of the CalCOFI grid, however, does permit us to examine these flows in general terms.

At those coastal stations where the depth of the bottom is less than 500 m, a reference level of 500 dbar is not available. For four such stations, 80.52, 90.28, 100.30, and 130.35, we have extrapolated the offshore horizontal density gradient at levels between the deepest observed levels and 500 dbar in order to estimate the surface flow. The extrapolation method is described by *Montgomery* [1941] and *Reid and Mantyla* [1976]. In choosing this approach, we note that it is sensitive to small errors in dynamic height. Most of the vertical shear and its variability, however, occur at shallow levels, and the sensitivity to small errors in dynamic height is ameliorated by smoothing with harmonic analysis. We feel that this procedure allows us to gain insight into the large inshore variability in current structure over the continental slope.

4. Results

4.1. *Dynamic Height*

Contour maps of dynamic height for the sea surface with respect to 500 dbar for four seasonal periods (Figure 2) show, to some degree, the variations in relative strength of near-surface flows. The strongest equatorward flow (CC) appears in spring and summer, whereas the strongest poleward coastal counterflow (IC) appears in fall and winter. The coastal counterflow is best organized during January; during April there is barely a vestige of this flow. By July, the Southern California Eddy has formed. This cyclonic eddy is geographically fixed about the shallow offshore banks of the Southern California Bight (Figure 1*a*). The CC has a large shoreward component just south of the international border [*Reid et al.*, 1963]. This flow divides; part flows northward as the nearshore limb of the Southern California Eddy or as the IC, and part flows southward along the coast. South of this division in flow, distributions for all seasons show a looping meander in the vicinity of Guadalupe Island (~29°N, 118°W).

Dynamic height at 200 m with respect to 500 dbar (Figure 3) shows patterns of seasonal flow similar to those at the surface. The equatorward flow is, however, considerably weaker at this level, and the poleward flow is generally broader and more coherent. The poleward flow during April is limited in extent to southern California and a short distance north of Point Conception. During most of the year off northern Baja California, a greater portion of the CC turns shoreward and then poleward at this level than at the surface.

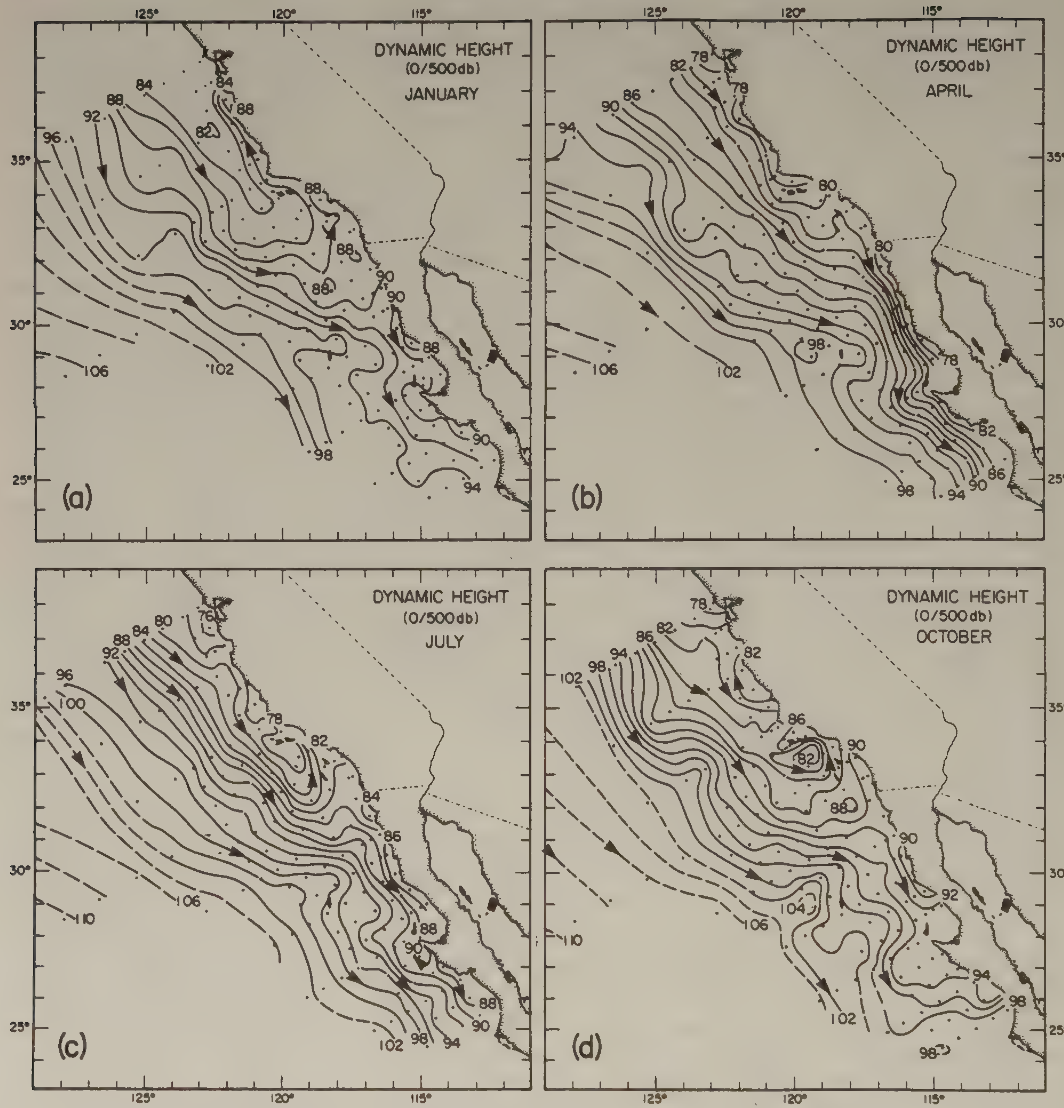
DYNAMIC HEIGHT (0/500db) JANUARY
(a)
DYNAMIC HEIGHT (0/500db) APRIL
(b)
DYNAMIC HEIGHT (0/500db) JULY
(c)
DYNAMIC HEIGHT (0/500db) OCTOBER
(d)
125°
120°
115°
35°
30°
25°

Fig. 2. Mean dynamic height (in dynamic centimeters) of the surface relative to 500 dbar for four periods (of approximately 60 days) centered about (*a*) January, (*b*) April, (*c*) July, and (*d*) October [from *Lynn et al.*, 1982]. Contour interval is 2 dyn cm.

Dynamic height also can be used to define regions where the influence and phasing of the geostrophic dynamics differ markedly. A coastal region, an offshore region, and a transition zone between them are readily identified by variations in the dynamic height of the surface with respect to 500 dbar (Figure 4). There is a seasonal tilting of the sea surface shown by the difference in dynamic height between the mean distribution for January 15 and that for July 15 (Figure 4*a*). Although the sea surface falls as much as 6 dyn cm in a band within 200 km of the coast during the first half of an average year, it rises an equivalent amount in the offshore region during the same period. Between these two regions there is a zone with little or no change in dynamic height. The full range of the seasonal variation (the harmonic highs minus the lows, regardless of date) produces a similar pattern (Figure 4*b*). The seasonal range exceeds 9 dyn cm along the coast and in the offshore region; a minimum, generally less than 5 dyn cm, forms a trough in this distribution centered approximately 200 km offshore. In the offshore region the seasonal minimum occurs in winter (Figure 4*c*). In the coastal zone it occurs some 4 months later. In the transition zone the seasonal cycle is weaker and erratic.

There is a band of high values >|4| dyn cm (the hatched area in Figure 4*d*) in the distribution of standard deviation about the overall record of dynamic height (i.e.,

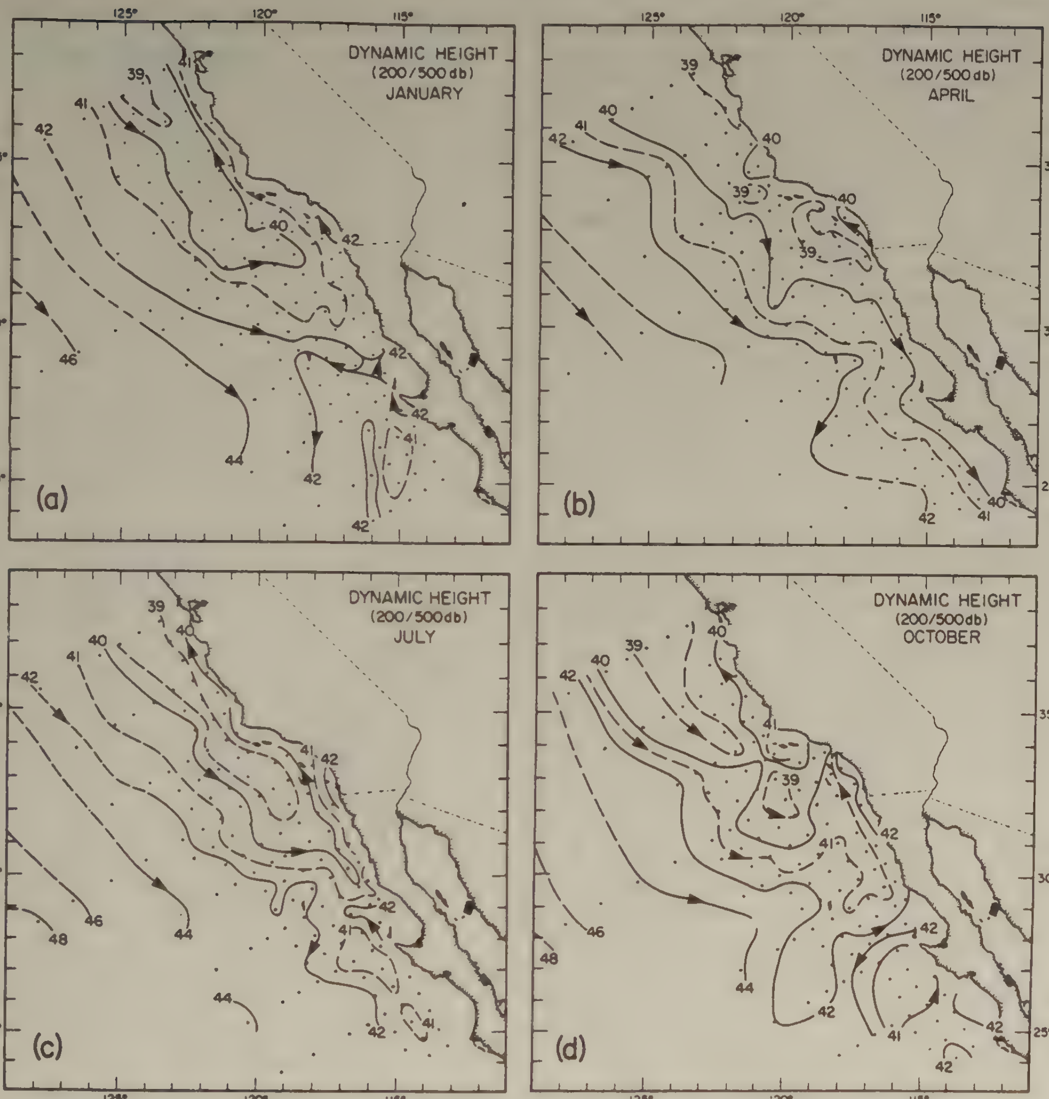
125°
120°
115°
35°
30°
25°
DYNAMIC HEIGHT (200/500 db) JANUARY
(a)
39
41
42
40
46
44
DYNAMIC HEIGHT (200/500 db) APRIL
(b)
40
39
41
42
DYNAMIC HEIGHT (200/500db) JULY
(c)
48
46
44
DYNAMIC HEIGHT (200/500db) OCTOBER
(d)

Fig. 3. The same as Figure 2 except for 200 m relative to 500 dbar. Contour interval is 1 dyn cm.

seasonal cycle not removed) in the transition zone between the coastal and offshore regimes. This band of high standard deviation in dynamic height coincides with the transition zone defined above. In general, in the zone where standard deviation in dynamic height is a maximum, its seasonal variation is a minimum.

4.2. *Surface Flow and Characteristics*

4.2.1. *California Current and Inshore Countercurrent.* Vertical sections of geostrophic velocity relative to 500 dbar along CalCOFI lines 70, 90, and 110 for odd months are given in Figures 5, 6, and 7, respectively. *Chelton* [1984] presents a figure similar to Figure 5, but his values differ from ours. His notation of station spacing given in kilometers is in error (too low) by the ratio of statute miles to nautical miles, which possibly accounts for his values appearing of the order of 10 to 20% higher than ours. (His conclusions, however, were not affected by this error.) *Lynn et al.* [1982] also give similar figures which were derived from arithmetic means.

Several generalizations about the California Current and Inshore Countercurrent can be made from the velocity sections (Figures 5, 6, and 7). The CC is a relatively shallow flow; the maximum velocity occurs at or near the surface. Flow exceeding 4 cm s^{-1} often does not extend below 150 m. In some seasons it occurs in bands defined by one or two pairs of stations separated by 75 to 150 km. The swiftest mean equatorward flow exceeds 20 cm s^{-1} at the surface of the inshore station pair of line 110 (Fig-

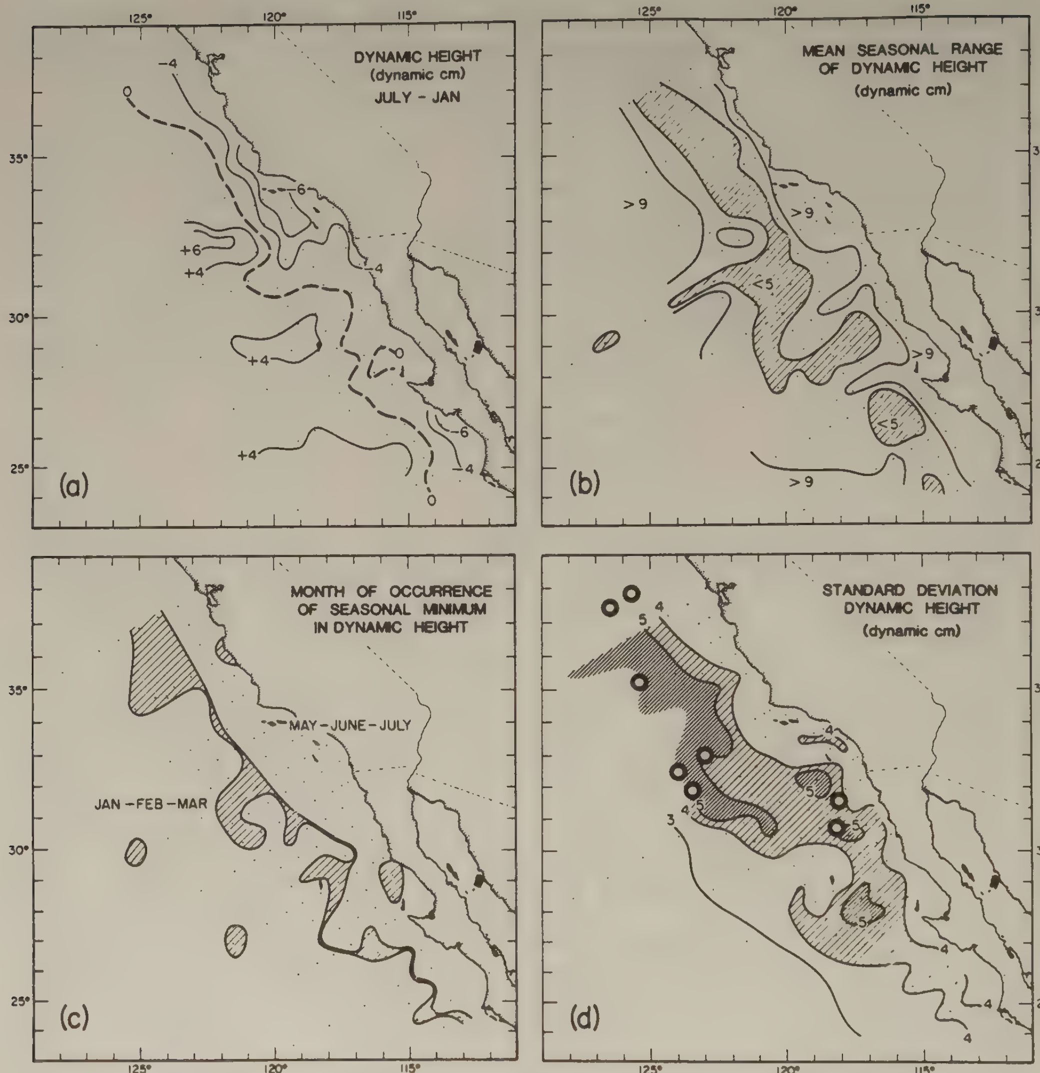
125°
120°
115°
35°
30°
25°
DYNAMIC HEIGHT
(dynamic cm)
JULY - JAN
-4
0
-6
+6
+4
-4
+4
0
-6
+4
-4
0
(a)
MEAN SEASONAL RANGE
OF DYNAMIC HEIGHT
(dynamic cm)
>9
>9
<5
>9
<5
>9
(b)
MONTH OF OCCURRENCE
OF SEASONAL MINIMUM
IN DYNAMIC HEIGHT
MAY - JUNE - JULY
JAN - FEB - MAR
(c)
STANDARD DEVIATION
DYNAMIC HEIGHT
(dynamic cm)
4
5
4
5
4
5
3
5
5
4
4
4
(d)

Fig. 4. (*a*) The difference between the mean fields of dynamic height for January 15 and July 15 (in dynamic centimeters). The zero line is shown dashed. (The characteristics depicted in Figures 4*a*–4*d* refer to dynamic height of the surface relative to 500 dbar. (*b*) The range of dynamic height derived from harmonic analysis (in dynamic centimeters). Range less than 5 dyn cm is hatched. (*c*) The months of occurrence of the seasonal minimum in dynamic height. Most months fall into two periods that are geographically separated. Those months that fell in neither period are separated by contours and hatched. (*d*) The standard deviation of dynamic height for the entire record of each station (i.e., seasonal variation was not removed). Standard deviation greater than 4 is hatched; standard deviation greater than 5 is densely hatched. The heavy circles give location of mesoscale eddies confirmed by independent studies.

ure 7). The IC, when it exists, is very narrow. Generally, where it exceeds 4 cm s^{-1}, it is defined solely by the inshore pair of stations along a given CalCOFI line. Typically, this inshore station spacing is about 30 to 50 km.

Seasonal variation in the strength and position of the high-velocity bands of these flows is more easily seen in plots of surface flow (0/500 dbar) perpendicular to each of the cardinal lines versus month (Plate 1). (Plate 1 can be found in the separate color section in this issue.) Such patterns of surface flow show strong regional differences. In one sense, each graph has some characteristics that are local in nature. The simplest of possible divisions consists of central California, southern California, and Baja California regions.

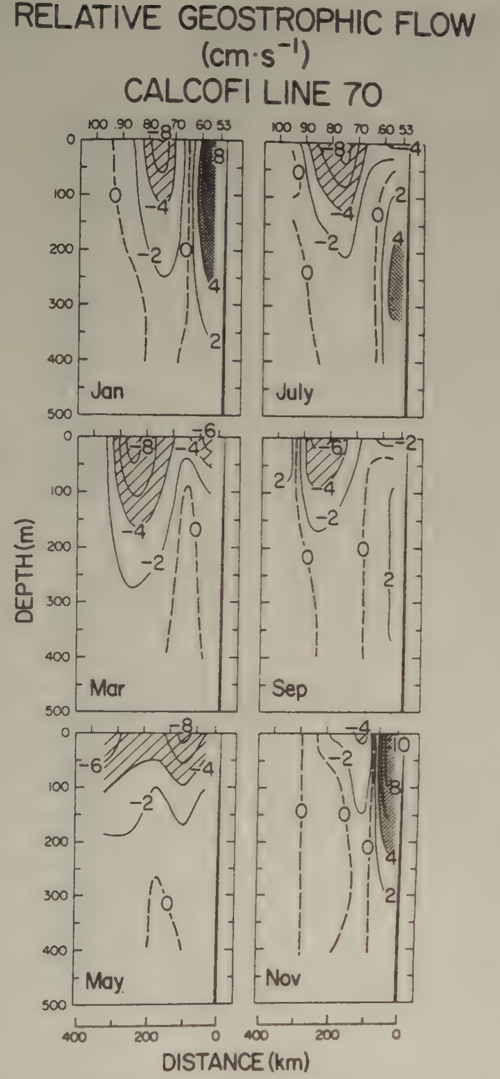

Fig. 5. Geostrophic velocity (in centimeters per second) relative to 500 dbar for odd months along CalCOFI line 70 (see Figure 1). Contour interval is 2 cm s^{-1}. Equatorward flow in excess of 4 cm s^{-1} is hatched. Poleward flow in excess of 4 cm s^{-1} is stippled.

Central California (lines 60, 70, and 80): The core of the surface equatorward flow is strongest approximately 200–300 km offshore with peak velocities occurring in the latter half of the year (Figure 5 and Plate 1). The inshore flow reverses direction seasonally; it is poleward in winter. The strongest inshore equatorward flow occurs in April–May at all three lines. Line 60 and line 80 both show semiannual variability in the nearshore region.

Southern California (line 90): There are two peaks in equatorward flow that are temporally and spatially distinct off southern California (Figure 6 and Plate 1). One occurs in midyear centered 70 km west of the offshore shallow bathymetric ridge (found at station 90.50, which is 173 km from shore). The second peak occurs in midwinter 180 km farther west. A line of zero flow lies above the bathymetric ridge. Shoreward of the bathymetric ridge, the poleward flow has two peaks: one in summer in the center of the Southern California Bight and another in late fall along the coast. The flow within the bight is mostly poleward. Equatorward flow does occur at the coast in August–September and very weakly so in March–April. The juxtaposition of the strong flow and counterflow of June–August is a space-time representation of the Southern California Eddy. Between these flows, Tanner Bank (~32.8°N, 119.2°W) is as shallow as 20 m.

Baja California (lines 100, 110, 120, and 130): The core of the equatorward surface flow is strongest along the coast; the maximum occurs in March and April (Figure 7 and Plate 1). There is a strong seasonal variability in the coastal equatorward flow. The seasonal reversal of this inshore flow, however, is very weak or nonexistent, with the exception of line 130 where there is a winter IC.

During March through May there is a tendency for all coastal flow in all three regions to be equatorward. North of the border this corresponds to a "spring transition" in the direction of inshore flow [*Huyer et al.*, 1979]. South of the border, inshore surface flow is equatorward most of the year. This equatorward flow peaks during the period of "spring transition" (Plate 1). A secondary peak occurs in equatorward flow 200 km offshore about June–July in three of the four station lines which define the Baja California region. There is strong semiannual variability inshore on line 130; a second strong equatorward flow occurs along the coast in August–September.

4.2.2. *Near-surface characteristics.* The mean distribution of salinity for July on the surface where $\sigma_t = 25$ ($\delta_t = 297$ cl/ton $= 297 \times 10^{-5}$ ml/g) (Figure 8) demonstrates the well-defined tongue of low-salinity water which traces an offshore path roughly parallel to the coastline and oriented parallel to the mean geostrophic flow (Figure 2). A very similar salinity pattern is found in other months [*Lynn et al.*, 1982]. The $\sigma_t = 25$ surface intersects the sea surface near central California (marked by a bold line and shading in Figure 8). Elsewhere it lies in the upper gradient of the thermocline, about 60 m in the low-salinity core and 100 m near the western edge (see depth distribution of this density surface given by *Lynn et al* [1982, p. 395]). This pattern of salinity distribution does not differ in any fundamental way from the distribution of salinity at the sea surface. (Slightly lower salinity prevails where this surface coincides with the shallow minimum.) On this surface of constant density, however, the tongue of low salinity is also a tongue of low temperature because temperature and salinity uniquely define σ_t. Thus Figure 8 provides a clearer illustration of the transport of upper layer water characteristics than the sea surface temperature distribution would because sea surface temperature is markedly influenced by shallow wind-driven Ekman transport and surface heat exchange.

In the central California region the lowest salinity is found at the surface (line 60, Figure 9*a*). In the Baja California region the lowest salinity occurs in a well-defined subsurface (50 to 100 m) core [*Reid et al.*, 1958] which is

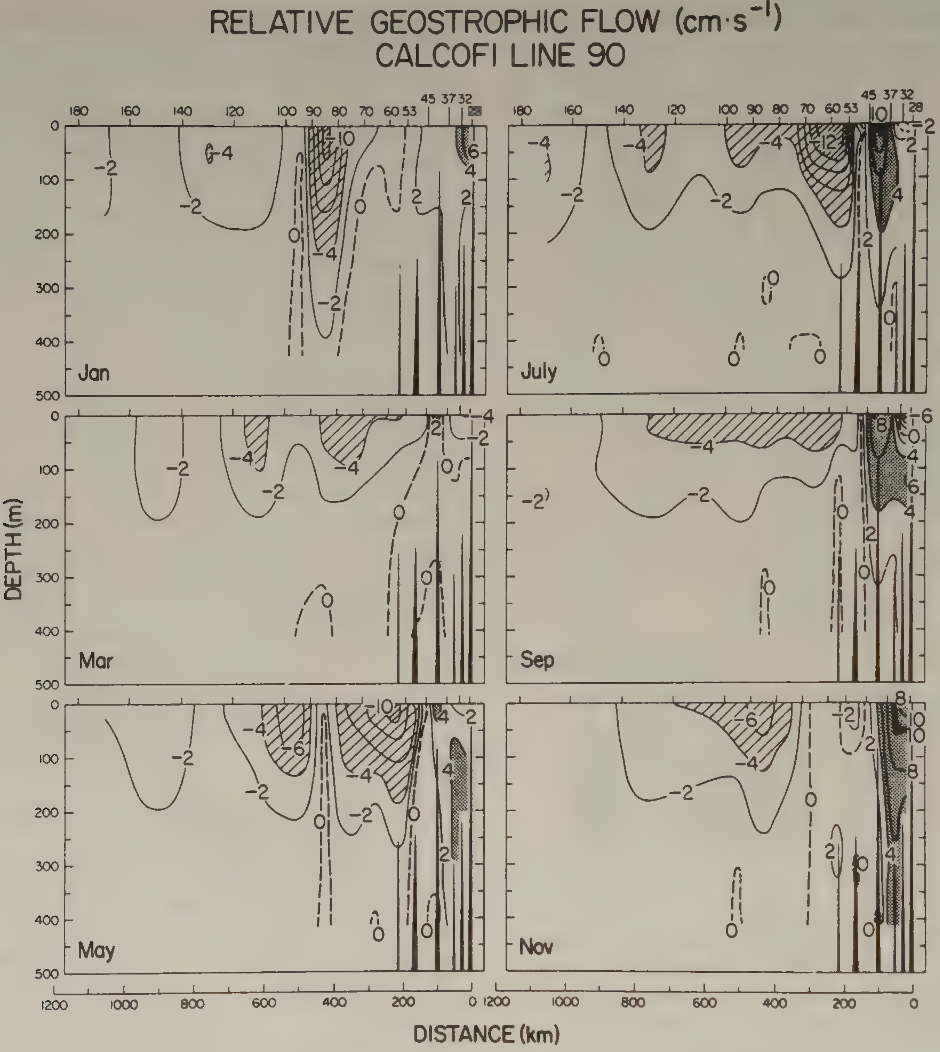

Fig. 6. Same as Figure 5 except for CalCOFI line 90.

close to the coast (line 110, Figure 9*c*). In the intermediate southern California region, the minimum salinity occurs at or very near the surface in July (line 90, Figure 9*b*). In fall there is a well-developed offshore subsurface salinity minimum (not shown). There is also a subsurface minimum inside the Southern California Bight [*Reid et al.*, 1964] caused by the recirculation of CC waters into the Southern California Bight. In summer the recirculation is intensified by the Southern California Eddy. The eddy is marked by the doming of higher-salinity waters at station 90.45 (Figure 9*b*).

In its equatorward path, the CC transports waters that have salinities as low as 33.7 to the vicinity of line 130 off southern Baja California (Figure 10). The subsurface salinity minimum has a larger lateral spread here than at line 110 and demonstrates a relatively large range of seasonal variation. In January, when there is a strong IC (Plate 1), waters with salinities below 33.8 are found offshore beyond the continental slope (hatched area in Figure 10). A strong equatorward flow coincides with the onshore return and surfacing of the salinity minimum layer in April and July. The October distribution is similar to that found in January, but unlike the January distribution, the surface inshore flow is strongly equatorward. The subsurface salinity minimum extends southward to 17°N [*Bennett*, 1963] and is carried westward in the North Equatorial Current [*Reid*, 1973; *Tsuchiya*, 1982].

In Figure 11 the lowest salinity found in the surface layer is plotted over the surface velocity graphs of Plate 1. For the most part, the (low-temperature) low-salinity core

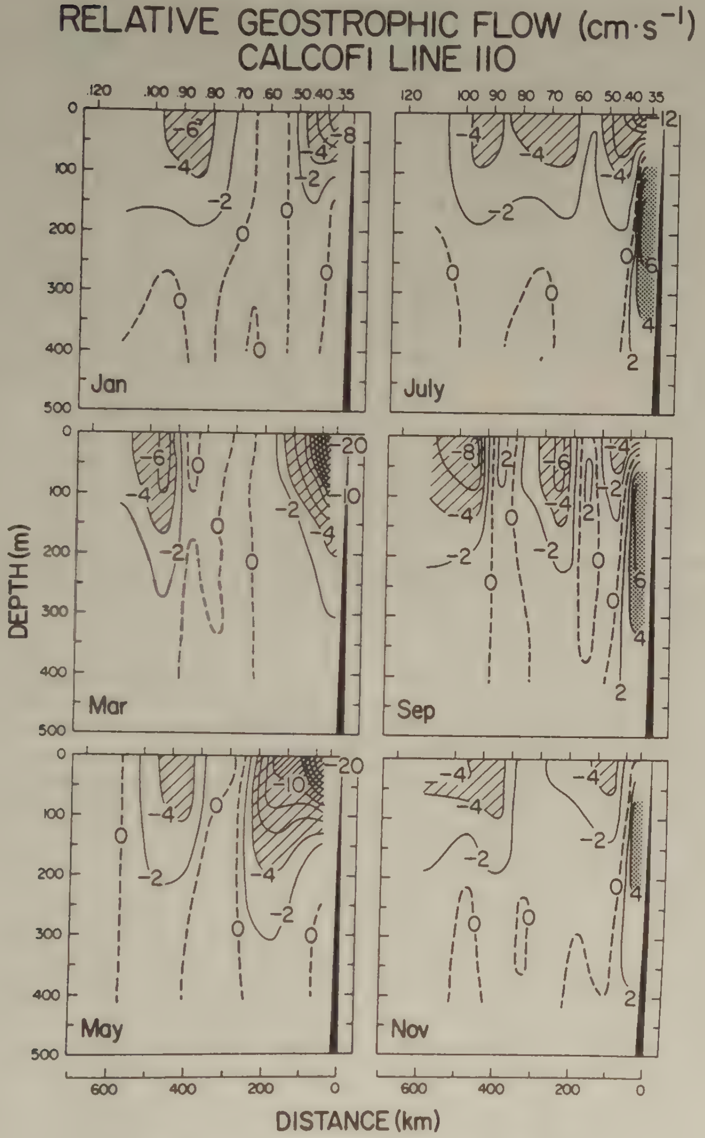

Fig. 7. Same as Figure 5 except for CalCOFI line 110.

falls in the regions of stronger equatorward flow. Despite the fact that salinity is measured at stations and velocity calculations are assigned between them, it is evident that the salinity minimum falls on the offshore side of the bands of high equatorward velocity. This suggests that there is greater infusion of salt into the low-salinity core from the higher-salinity coastal waters than from the offshore North Pacific Central waters. This pattern differs at line 90, where there are two strong flows and a double salinity minimum. The unique distribution of salinity at line 90 is caused by the upward displacement and mixing of deeper characteristics associated with the cyclonic circulation of the Southern California Eddy and the advection of low-salinity waters into the bight. This correspondence of strong flow and low salinity extends to depths of at least 100 m (Figures 5, 6, 7, and 9). Thus the low-salinity core is a good descriptor of the path of the California Current.

4.3. *Subsurface Flow and Characteristics*

4.3.1. *California Undercurrent.* The CU is a subsurface poleward flow. At 250 m, this poleward flow generally

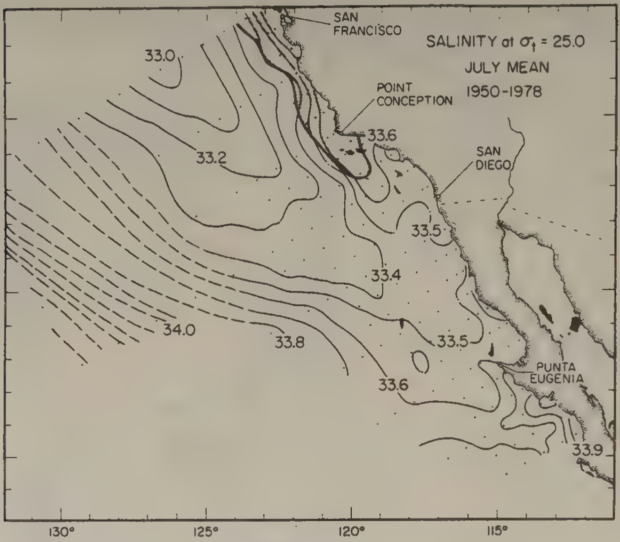
SALINITY at σ_t = 25.0
JULY MEAN
1950-1978
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
33.0
33.2
33.4
33.5
33.6
33.8
33.9
34.0
35°
30°
25°
130°
125°
120°
115°

Fig. 8. Mean salinity on the surface where σ_t = 25.0 for July [from *Lynn et al.*, 1982]. The intersection of this density surface with the sea surface is indicated by a bold line. Where density is less (shown shaded), surface salinity is given. Contour interval is 0.1.

does not extend beyond 100 km from the coast (Figure 3); at greater depths it may extend to greater distances [e.g., *Hickey*, 1979]. Observations [*Reid*, 1962, 1963; *Wooster and Jones*, 1970] show that the CU has a high-velocity core along the continental slope. The seasonal cycle of the core of the CU is illustrated in Figure 12 (dashed lines), together with the surface flow above it

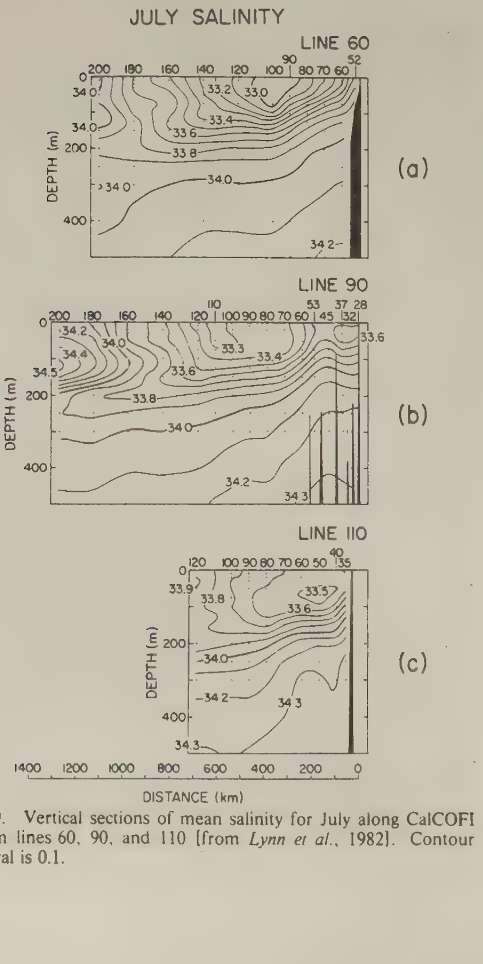

Fig. 9. Vertical sections of mean salinity for July along CalCOFI station lines 60, 90, and 110 [from *Lynn et al.*, 1982]. Contour interval is 0.1.

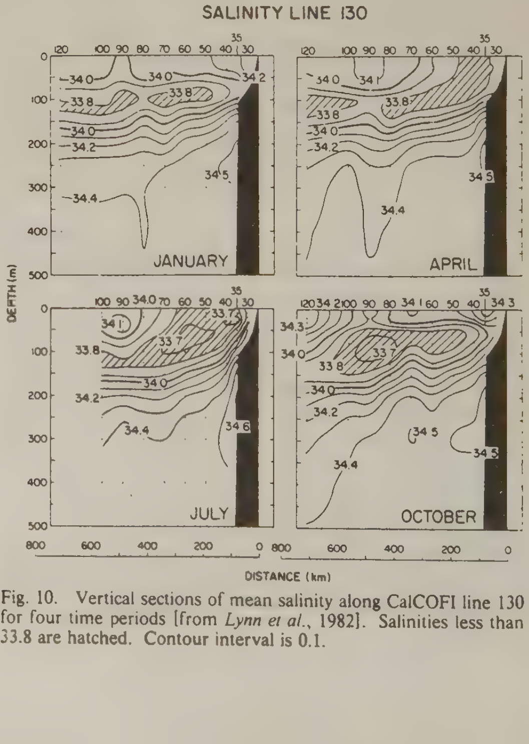

Fig. 10. Vertical sections of mean salinity along CalCOFI line 130 for four time periods [from *Lynn et al.*, 1982]. Salinities less than 33.8 are hatched. Contour interval is 0.1.

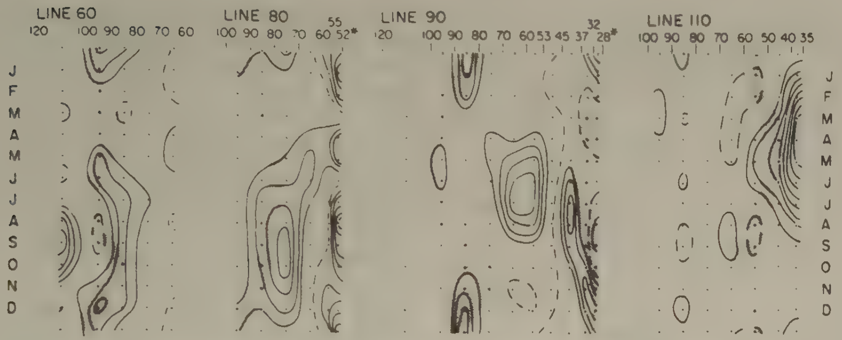

Fig. 11. The core of lowest-salinity California Current water (shaded) plotted on the velocity space-time graphs from Plate 1.

(solid lines). Relative geostrophic velocities were calculated using inshore pairs of stations, each reaching 500 m. Positive flow is poleward. At these station pairs the CU is defined as a subsurface maximum in poleward flow. Thus there is no CU when all flow is equatorward or when the maximum in poleward flow is at the surface or indistinguishable from the surface flow. The surface flow, when it is poleward, is labeled IC for Inshore Countercurrent; when it is equatorward, it is the CC.

In many places there is a tendency for flow to be poleward at some level year round. For the most part, this poleward flow is subsurface. At those places where there is a seasonal interruption, the interruption occurs for 2 or 3 months in spring (Figure 12). (Off southern Baja California there is also an interruption in fall (Figure 12*h*).) There is a strong semiannual variability in the CU off Central California (Figure 12*a*), off Point Conception (Figure 12*b*), and again within the Southern California Bight (Figure 12*d*) (see also *Hickey* [1979] and *Chelton* [1984]). This semiannual signal does not occur at the intermediate station line (Figure 12*c*) which lies seaward of Santa Rosa Island (~34°N, 120°W). This latter station pair is the only one in Figure 12 which is not adjacent to the coast. At many locations the CU diminishes in strength from January through March, and its core, defined by the subsurface maximum in poleward flow, is found at increasingly greater depths (Figure 13). From March through May at most coastal locations, the CU is either nonexistent or extremely weak (Figures 12 and 13). The correspondence of the weakening with the deepening of the CU suggests that the interruption of the CU in places could result from the assumption of zero flow at 500 dbar. After it reforms or increases in strength, in late spring and summer, it is found at increasingly shallower depths. In some instances the CU reaches a level where it is not discernible from the surface poleward current (e.g., Figure 12*a* and Figure 13*a*) (see also *Sverdrup et al.* [1942]). There are also long periods when the surface flow is equatorward, in opposition to the CU. In general, however, the geostrophic velocity at the sea surface is highly coherent with that at 250 m from central California to southern Baja California (Figure 12*a*–12*h*). *Chelton* [1984] observed this coherence north of the international border in relation to the upper 150 m. Further, he noted that an exception to this observation occurs at Point Conception (see Figure 12*b*). Over the outer continental slope the variability of the surface flow is annual, while that of the deeper flow is largely semiannual. A second exception is found at Punta Eugenia (Figure 12*g*). These two points are the major coastal capes in this study area. *Chelton* [1984] limited his study to the outer continental slope. An additional station, 80.52 (90 observations), falls over the inner slope at Point Conception. Although the sounding there is 220 m, the data record, for the purposes of time series analysis, is consistent to only 150 m. Geostrophic shear in the upper 150 m between stations 80.52 and 80.55 shows a very strong semiannual variability (Figure 12*i*). At Point Conception, therefore, the deeper outer slope flow is coherent with the surface flow over the inner slope. There is no inner slope CalCOFI station at Punta Eugenia with which to check for similar circumstances there. Because the amplitude of the variability in surface flow at Point Conception is much greater than that of the outer slope CU and because the surface flow lags the deeper flow by 1.5 months, shoreward extrapolation of the deeper flow produces a modest adjustment of the inshore surface geostrophic velocity (Figure 12*i*). This extrapolated velocity was used in Plate 1. There is a strong (11 cm s^{-1}) equatorward flow in spring and an equally strong (~13 cm^{-1}) poleward flow in August and again in January.

4.3.2. *Subsurface characteristics.* Distributions of characteristics on a surface of constant density that lies at middepths show the effects of transport at those depths. The 26.6 σ_t (δ_t = 145 cl/ton) surface lies between depths of 200 and 300 m along the coastal margin (Figure 14*a*). Peak velocity of the CU usually falls within or close to this range of depth during summer months and sometimes during winter (Figure 13). Distributions of salinity (and implicitly temperature) and oxygen on this density surface (Figures 14*b*, and 14*c*) illustrate the flow of the CU (Figure 12). Warm, saline, low-oxygen waters from subtropical latitudes are transported northward in a band along the coast. *Wooster and Jones* [1970] illustrated salinity in this manner for a July cruise. The extremes of high salinity, high temperature, and low oxygen found along the coastal margin are modified by lateral mixing with waters that are transported southward beyond 200 km offshore of California. The gradients of characteristics and isopleths of

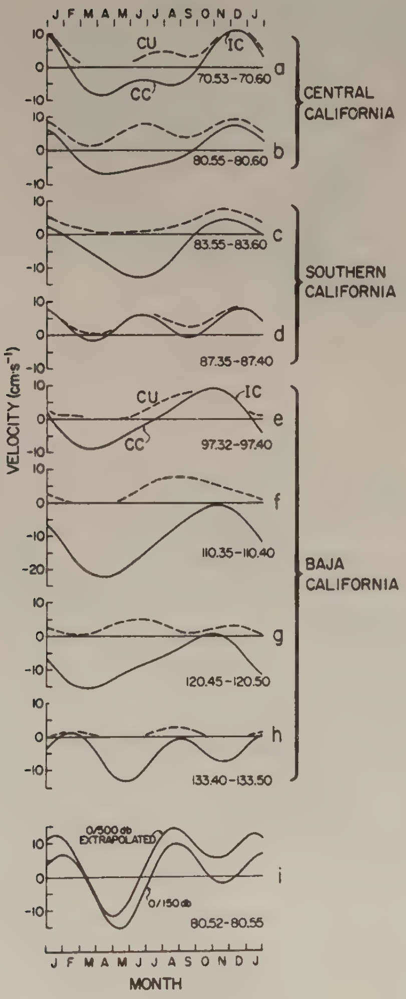

Fig. 12. (*a–h*) Relative geostrophic velocity (in centimeters per second) versus month for the California Current (CC) or surface Inshore Countercurrent (IC) (solid lines) and California Undercurrent (CU) (dashed lines) for station pairs from central California to southern Baja California that can be located in Figure 1. Each station pair lies adjacent to the continental shelf where there is at least 500 m of water. The CU is defined as a subsurface maximum in poleward flow; where the depth is less than 75 m it is not differentiated from the IC. (*i*) Two versions of relative geostrophic velocity at the surface over the inner continental slope near Point Conception (water depth 220 m). One uses a reference level of 150 dbar, and the other, based upon the shoreward extrapolation of deep shear, uses 500 dbar.

dynamic height suggest that in July this incursion of offshore waters is stronger off southern California and northern Baja California than elsewhere.

Depth, temperature, oxygen, and geostrophic velocity interpolated to levels where $\sigma_t = 26.6$ are plotted on a grid of distance along the cardinal lines versus time for an annual cycle. Contoured space-time graphs of these characteristics (Plate 2) demonstrate the relation between the seasonal flow of the CU and the characteristics it transports. (Plate 2 can be found in the separate color section in this issue.) This relation is particularly evident in the high-gradient region along the coastal margin. Along any given line there is a strong space-time coherence between characteristics. For example, the patterns for temperature and oxygen at line 110 (Plate 2*d*) are very similar. There is also a larger-scale space-time coherence both for a given characteristic and between characteristics from Point Sur (line 70) to Punta Eugenia (line 120) evidenced by the overall general similarity of most graphs in Plate 2. The flow of waters from the south along the coast carries the characteristics of higher temperature, higher salinity, and lower oxygen. Seasonally, the variation in strength of this flow results in a poleward extension or retreat of these extreme characteristics. The CU disappears at line 70 (Plate 2*a*) during March through May. Its disappearance slightly precedes the shallowest occurrence of the $\sigma_t = 26.6$ isopycnal (April through June) and the presence of the seasonally coolest and most oxygenated waters found at the coast (May and June). At line 80 (Plate 2*b*) there is a stronger semiannual signal in the CU than at line 70, as is evidenced in the corresponding temperature and oxygen distributions. Here the two strong pulses of the CU each precede both of the minima in oxygen and maxima in temperature. (The secondary temperature maximum is weak and is not revealed in the contours used in Plate 2*b*.) The effects of the summer development of the Southern California Eddy are evident at depth along line 90 in the vertical displacement of the density field (Plate 2*c*). The relative geostrophic velocity field shows that the influence of the eddy reaches 220 m. In fact, at $\sigma_t = 26.6$ the geostrophic velocity has essentially the same pattern, but at reduced values, as it has at the surface (Plate 1). The seasonal variation of nearshore characteristics within the Bight is not as strong as that observed off central California. Further south and inshore at line 110 (Plate 2*d*) there is a simple annual cycle; the CU disappears in spring 1 month before the minimum in

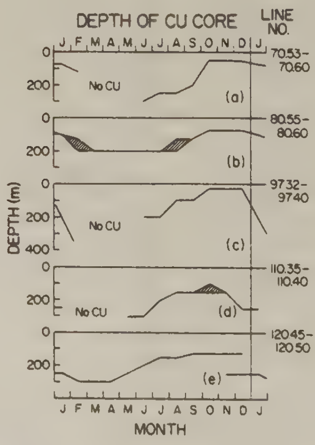

Fig. 13. Depth of the high-velocity core of the California Undercurrent versus month for some of the graphs of Figure 12.

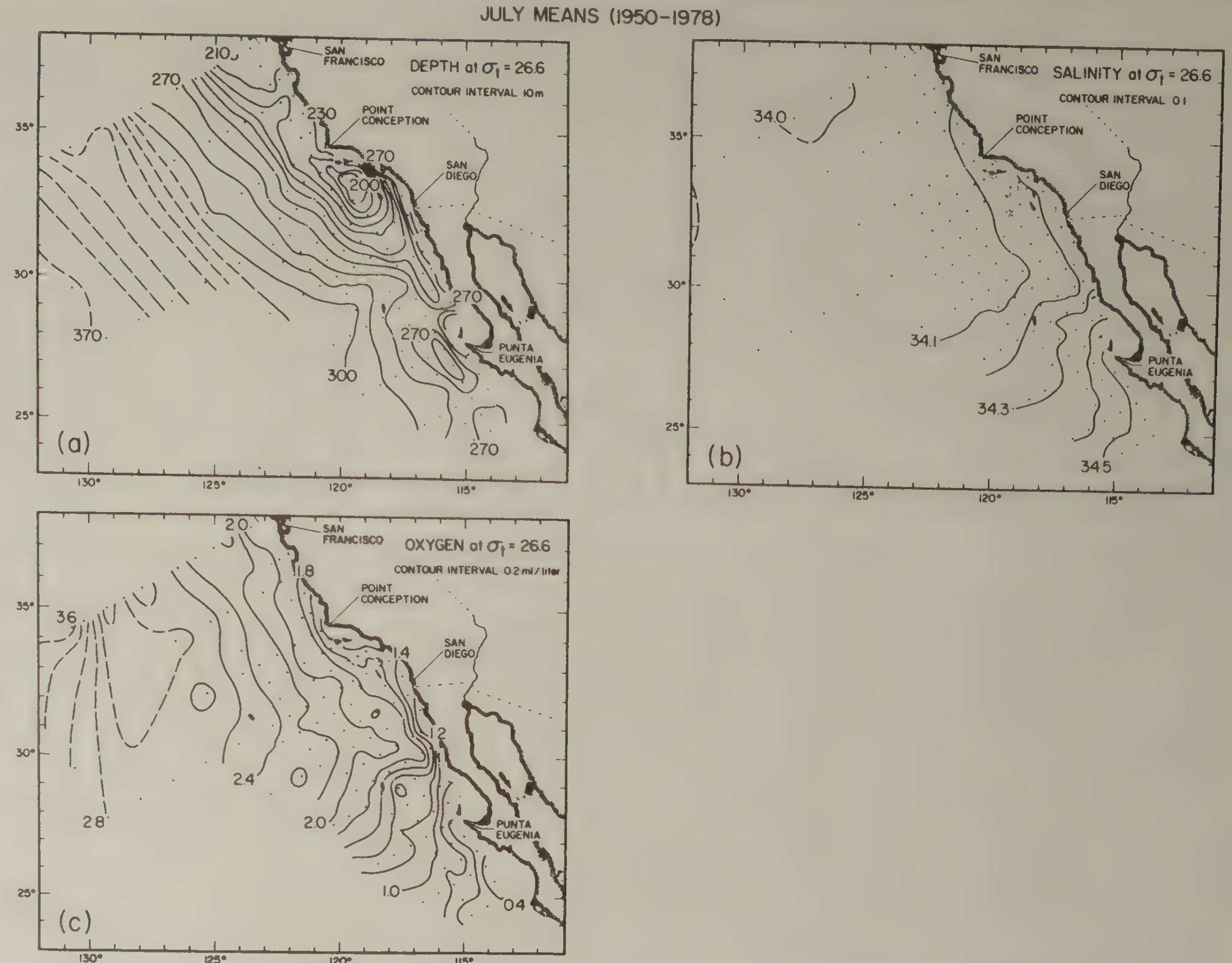
JULY MEANS (1950-1978)
DEPTH at σ_t = 26.6
CONTOUR INTERVAL 10m
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
210
270
230
200
300
370
(a)
SALINITY at σ_t = 26.6
CONTOUR INTERVAL 0.1
34.0
34.1
34.3
34.5
(b)
OXYGEN at σ_t = 26.6
CONTOUR INTERVAL 0.2 ml/liter
2.0
1.8
1.4
1.2
1.0
0.4
2.4
2.8
3.6
(c)
35°
30°
25°
130°
125°
120°
115°

Fig. 14. (*a*) Mean depth (in meters) for July of the density surface σ_t = 26.6, (*b*) mean salinity, and (*c*) mean oxygen concentration (in milliliters per liter) for July on the σ_t = 26.6 surface (All from *Lynn et al.* [1982]).

temperature and maximum in oxygen. Distributions at line 120 (Plate 2*e*) show structure in coastal flow and characteristics similar to those on line 110. These distributions also show a response to the large-scale cyclonic eddy that strengthens in fall and whose center lies to the southeast of Punta Eugenia (Figure 3). The northern limb of this eddy carries warm, low-oxygen waters at least 550 km offshore during October through January (Plate 2*e*).

The foregoing description assumes that with the depth range of the σ_t = 26.6 surface the seasonal variation in advection dominates other processes affecting the seasonal variation of oxygen concentrations. The strong match of the seasonal patterns of oxygen to those of temperature suggest that to a first order, our assumption is correct.

5. DISCUSSION

5.1. *Dynamic Height*

The long-term, large-scale mean seasonal patterns in the surface (Figure 2) and subsurface (Figure 3) dynamic heights reflect the seasonal variability of the California Current, Inshore Countercurrent, and California Undercurrent. These patterns are similar to those presented by *Wyllie* [1966] and discussed by others [e.g., *Hickey*, 1979; *Chelton*, 1982; *Simpson*, 1984*b*].

The mean seasonal range of dynamic height (Figure 4*b*) and the months in which the seasonal minimum in dynamic height occurs (Figure 4*c*) define a coastal region, an offshore region, and a transition zone between them. In the offshore region the seasonal minimum occurs in winter, as would be expected from the effects of seasonal cooling. This is consistent with the large-scale open ocean distribution of dynamic height found in the eastern temperate North Pacific. There, seasonal changes in dynamic height are tied to the heating and cooling cycle [*Wyrtki*, 1975]; the minimum occurs in winter, the maximum in summer. Wyrtki finds that seasonal variations in dynamic height caused by changes in current patterns in the open ocean at temperate latitudes are generally much less than those caused by large-scale heating-cooling cycles. Shoreward of 200 km the opposite is true (Figures 4*b* and 4*c*). Here, the nearshore region has a seasonal variability in dynamic height that is dominated by processes other than the heating-cooling cycle [*Reid and Mantyla*, 1976]. In fact, seasonal variability in dynamic height in this domain is controlled by the seasonal occurrence of the IC and seasonal intensification of the CU (Figures 12 and 13). In the transition zone the month of occurrence of seasonal minimum in dynamic height has no pattern. It does not correspond to either periods of open ocean surface cooling or periods of inshore alterations in current flow (Figure 4*c*). It is unlikely that the ridge of high values in standard deviation of dynamic height (Figure 4*d*), coincident with the transition zone, would result simply from the combined influence of the neighboring regimes, each having a different physical forcing mechanism. Recurrent mesoscale eddies have been observed within this zone [e.g., *Bernstein et al.*, 1977; *Simpson et al.*, 1984]. Because the eddies have a large anomaly in dynamic height, the spatial and temporal variations of such eddies would readily boost the nonseasonal variation in dynamic height. Hence we suggest that the band of high standard deviation and of minimum seasonal range in dynamic height defines a zone in which there is a frequent occurrence of mesoscale eddies. Several independent sets of data support this interpretation. Maps for individual CalCOFI cruises show occurrences of enclosed contours and meanders within this transition zone that can be interpreted as eddies [*Wyllie*, 1966; *Burkov and Pavlova*, 1980] (see also the ongoing series of CalCOFI data reports). Some of these meanders are probably not eddies. There are, however, frequent occurrences of singular stations at which the dynamic height is significantly different than surrounding values; these singularities provide an unambiguous interpretation of an eddy. It is these latter realizations that contribute heavily to the formation of the band of high standard deviation in Figure 4*d*. Eddies whose signatures impress the long-term CalCOFI record must have length and persistence scales similar to those of the offshore eddies studied by *Simpson et al.* [1984]: 100 to 200 km and several weeks to several months. Other studies in the California Current system [*Reid et al*, 1963; *Bernstein et al.*, 1977; *Simpson et al.*, 1986; *Haury et al.*, 1986] also show mesoscale eddies that fall within this offshore band of high standard deviation in dynamic height. The positions of eddies from these studies and from eddies evident in published satellite-derived imagery [*Abbott and Zion*, 1985; *Lynn and Svejkovsky*, 1984] are plotted as circles in Figure 4*d*. All these data support the hypothesis of a transition zone populated with mesoscale eddies which lies between the coastal and open ocean flow regimes of the California Current system.

The interpretation of this zone of high standard deviation and low seasonality in dynamic height solely as an avenue of eddies is inappropriate. In general, the core of the CC lies within this band. The current core is defined by the relatively swifter meandering equatorward flow (Figure 2 and Plate 1) and the presence of the more extreme values of those measurands that characterize its source waters: low salinity and low temperature (Figure 8). Eddy-current field interactions are discussed in more detail in the following section.

5.2. *California Current and Inshore Countercurrent*

The California Current is an offshore, near-surface, permanent, equatorward flow. In the long-term average, this flow is slow, broad, and diffuse (Figure 2). The core of this flow is characterized by waters having relatively low temperature, low salinity (Figure 8), and high dissolved oxygen [e.g., *Lynn et al*, 1982]. Typical mean speeds are 4–12 cm s^{-1} in the upper 150 m of the water column (Figures 5, 6, and 7). Off central and southern California, the core of the CC generally occurs about 300–400 km offshore. Off Baja California, the core of the CC approaches within 200 km of the coast (Figure 2). The far offshore, semipermanent, high-salinity frontal structure, which is the southeastern extension of the Subarctic Frontal Zone (i.e., the California Front) is a good working definition of the western boundary of the CC proper. With this definition, the western boundary of the CC proper occurs about 900 km offshore.

The Inshore Countercurrent is a poleward flow which is confined primarily over the continental shelf and slope. Off central and southern California, it can extend as far as

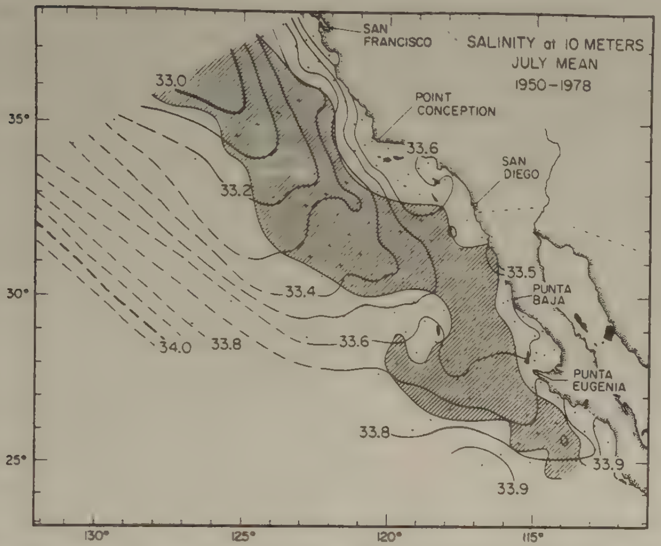

Fig. 15. Standard deviation of dynamic height (> ± 4 dyn cm) from Figure 4*d* (shown hatched) plotted over on the long-term mean 10-m salinity for July [from *Lynn et al.*, 1982].

100 km offshore (Figure 2). It is confined to a more narrow coastal domain off Baja California, and in fact, off portions of northern Baja California there appears to be no poleward surface flow in the average (Figure 12) (unless it falls shoreward of our station pattern). There is a pronounced seasonal cycle in the appearance and strength of the IC (Figure 12 and Plate 1). Generally, the periods of maximum strength in the flow of the IC correspond with the periods of maximum strength in the flow of the California Undercurrent (Figures 12 and 13). In some months the poleward surface flow of the IC is spatially discontinuous (Figure 2), giving the appearance of inshore cyclonic eddies. During those periods when the inshore surface flow is equatorward, this flow is part of the overall flow of the California Current; along the coast the strongest equatorward flow generally occurs in spring.

"Spring transition" events are defined at nearshore locations by abrupt decreases in temperature and reductions in (or reversals of) the poleward flow over a considerable depth [*Huyer et al.*, 1979]. The CalCOFI data and the harmonic analysis used here cannot resolve the abrupt nature of the spring transition. We do note, however, the apparent simultaneity in springtime of either a reversal of the IC or an intensification of the CC along the coast from San Francisco to southern Baja California (~1500 km distance). This finding supports the conclusion by *Brink et al.* [1984] that the forcing mechanism for the spring transition occurs on a large spatial scale and does not seem to be associated with a coastally trapped wave.

In Figure 15 the standard deviation of dynamic height taken from Figure 4*d* is shown superimposed upon the long-term mean distribution of salinity at 10 m for July. This band of maximum in standard deviation, which defines the transition zone between coastal and oceanic regimes, generally lies within the region of offshore low-salinity core. The low-salinity core is itself a manifestation of the mean flow of the CC. Offshore mesoscale eddy activity significantly contributes to this band of maximum in standard deviation of dynamic height. There is also a contribution from the mean flow field. A region of enhanced gradient of dynamic height is found where the maximum flow occurs (e.g., Figure 2). Spatial variations, especially nonseasonal, in the position of the core of flow (i.e., meanders) create a maximum in standard deviation of dynamic height about the high-gradient region. These variations in the core of flow may themselves be associated with eddy activity. The combined distribution of salinity and standard deviation of dynamic height (Figure 15) supports the conclusion that there is a significant interaction between the CC and the offshore eddy field. The offshore eddy field in this band of maximum deviation is composed primarily of anticyclonic eddies [e.g., *Bernstein et al.*, 1977; *Burkov and Pavlova*, 1980; *Simpson et al.*, 1986]. Such eddies would tend to intensify the flow of the CC on the shoreward side of the eddy and diminish the flow of the CC on the westward side of the eddy. The effect of such an eddy-current interaction would be to produce a broadened core of low salinity by mixing and to displace the peak velocities of the CC shoreward of the low-salinity core (Figure 11).

Hickey [1979] discusses the mean flow of the CC based upon monthly arithmetic averages of dynamic height (e.g., her Figures 6 and 8). The averages she uses are from *Wyllie* [1966] and cover a period of 15 years (1950–1964). She hypothesizes that there are two distinct regions of strong southward flow separated by a region of reduced southward, or even northward, flow. Wyllie's maps of mean monthly dynamic topography, however, frequently lack sufficient numbers of observations (> 3 per month) with which to calculate a meaningful average. This is especially true north of San Francisco and at distances greater than 400 km from shore. The distributions of mean dynamic height we present (Figure 2) are based on arithmetic averages covering a period of 29 years (1950–1978). Evidence for multiple branches is far less clear in this updated version of the mean dynamic height field. Our interpretation of eddies (cyclonic or anticyclonic) imbedded in the CC core (Figures 4*d* and 15) would produce a strengthening of the equatorward flow on one side of the eddies and a weakening or reversal on the other side. Hence in a long-term average, this weakening of current in midstream could produce the appearance of branching of the CC. There is no evidence of branching in the distributions of water characteristics (Figure 8); lateral entrainment and subsequent mixing of inshore and offshore waters by the eddies [*Simpson*, 1984*c*; *Simpson et al.*, 1986; *Haury et al.*, 1986; *Liu et al.*, 1987] would, in a long-term average, destroy such evidence.

5.3. *California Undercurrent*

At depth, poleward flow occurs along the California–Baja California coast and, in most seasons, offshore to about 150 km. The highest speeds in the core of this flow are found along the continental slope. When and where the subsurface poleward flow reaches shallow levels ($\leqslant 50$ m), it is barely distinguishable from the surface Inshore Countercurrent. This definition of the CU is consistent with direct current observations [e.g., *Reid*, 1962; *Wooster and Jones*, 1970] which show that the core of the CU is a narrow ribbon of high-speed (~ 30 cm s^{-1}) flow about 20 km in width and 300 m thick pressed against the continental slope.

The highest seasonal mean velocities of the CU are about 8 to 10 cm s^{-1} at various locations between San Francisco and Baja California (Figure 12). Poleward velocities exceeding 4 cm s^{-1} generally are confined to within 60 km of the coast off central and southern California (shaded in Figures 5 and 7). The CU also occurs along the continental slope in the Southern California Bight (Figure 6). Its appearance there, however, is complicated during summer and early fall by the strong poleward surface flow of the inshore limb of the Southern California Eddy. This inshore limb is centered 100 km offshore and recirculates the low-salinity waters of the offshore CC (Figure 11). Thus these recirculated waters are readily distinguishable from the more saline, subsurface poleward flowing waters of the CU.

The calculations of mean velocity (Figure 12) largely underestimate the high speeds of the narrow (20 km wide) core structure of the CU. They do, however, provide a general description of this current and its strong seasonal variation. Some of these seasonal graphs have a simple annual cycle; others have a strong semiannual cycle. The element in common among most of these graphs is the peak in velocity which occurs during late fall to early winter in the CU and/or IC, or a minimum in velocity where the surface flow is equatorward. This common element may be indicative of a larger-scale variation in driving forces than that which causes the more localized semiannual events evident within the bight (Figure 12*d*) and in the CU along central California (Figures 12*a* and 12*b*). In Figures 12*a* and 12*b* a second peak occurs in the CU-IC in summer. The summer peak of the CU and IC in the bight (Figure 12*d*) is apparently a response to the spin-up of the Southern California Eddy several tens of kilometers to the west. The summer peak in the CU at Point Conception and farther north may be a downstream (poleward) effect of this spin-up as evidenced by the northward decrease in the relative strength of this summer peak [see *Chelton*, 1984]. The very strong semiannual cycle of the IC off Point Conception (line 80) is evidenced in Plate 1, which uses an inshore station pair shallower than 500 m. The velocity graph for stations 83.55 and 83.60 off southern California (Figure 12*c*) shows a simple annual cycle. These stations are not located in the coastal zone; rather, they fall immediately seaward of the outer banks of the Southern California Bight (Figure 1*a*) and thus are unaffected by the summertime appearance of the Southern California Eddy.

Along southern Baja California the graphs of the annual cycle of velocity (Figures 12*g* and 12*h*) show considerably less coherence in their patterns. The large eddy off Punta Eugenia and complex patterns in the 200/500 dbar dynamic topography (Figures 2 and 3) demonstrate localized patterns in the seasonal cycles of the coastal flow. The large capes and partial embayments in the coastline and the proximity of the end of the Baja California peninsula contribute to these strong intraregional differences in patterns of flow.

We have chosen the $\sigma_t = 26.6$ ($\delta_t = 145$ cl/ton) density surface to illustrate the distribution of deeper-water characteristics associated with the core of the CU because this density surface falls within a depth interval where the core is found. *Wooster and Jones* [1970] chose nearly the same surface ($\delta_t = 150$ cl/ton) for the same reasons. The panels of Plate 2 show the seasonal variation in the distributions of these characteristics from central California to Baja California. Lowest dissolved oxygen concentration is centered over the continental slope throughout this domain. The domain of low-oxygen water also is a domain of warm, saline water. (Warm waters imply saline waters on a surface of constant density.) These extremes of low oxygen, high temperature, and high salinity occur within the region of maximum subsurface poleward flow.

The seasonal variation in the extremes of these characteristics also coincides temporally with the seasonal variation in the strength of the CU core. This seasonal variation is particularly evident in the high-gradient regions along the coastal margin. Here, the seasonal increase in transport of waters from the south along the coast causes extremes in the high temperature and salinity and low oxygen; the seasonal slackening in transport of these waters results in the lessening of the extremes. There is no CU at line 70 (Plate 2*a*) during March through May. Its disappearance slightly precedes the shallowest occurrence of $\sigma_t = 26.6$ (April through June) and the presence of the coolest and most oxygenated waters at the coast (May and June). May and June are also the months of strongest upwelling [*Bakun*, 1975]. At line 80 (Plate 2*b*) there is a stronger semiannual signal to the CU than at line 70, as is evidenced in the corresponding temperature and oxygen distributions. Here the two strong pulses of the CU each precede both of the minima in oxygen and maxima in temperature. (The secondary temperature maximum is weak and is not revealed in the contours used in Plate 2*b*.) These contour patterns also demonstrate the strong large-scale interrelationship between corresponding fields. For example, the tempera-

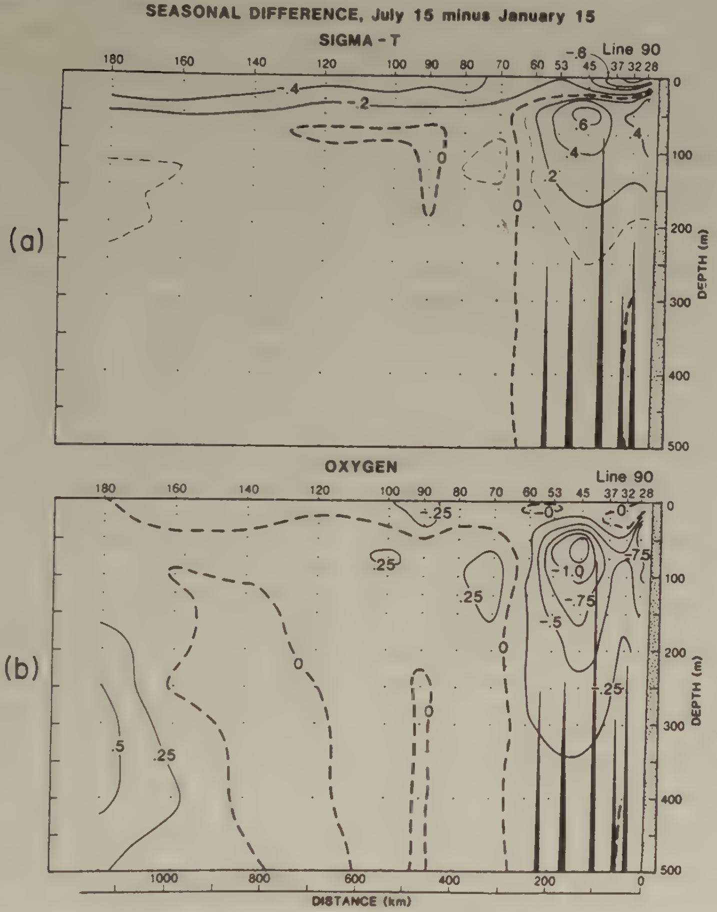

Fig. 16. (*a*) Vertical section of the difference between mean fields of σ_t along line 90 for January 15 and July 15. (*b*) The corresponding plot for oxygen difference.

ture (salinity) and oxygen patterns are nearly identical over the entire CalCOFI region.

There is usually a peak in the flow of the CU during late fall or in the IC where and when the CU shoals and becomes a surface current (Figure 13). At most locations the peak velocities of the IC or, where appropriate, the minimum values in the inshore CC, coincide with this strengthening and shoaling of the CU (Figures 12 and 13). This coincidence suggests that the IC is a surfacing of the CU. Additionally, the period of maximum in the IC flow also corresponds to the period of reduced surface wind stress [*Nelson*, 1977]. During this same period the distribution of inshore salinity on the deep $\sigma_t = 26.6$ density surface (Plate 2) and the shallower $\sigma_t = 25.8$ surface [*Lynn et al.*, 1982] is higher than during spring and summer. Likewise, during this period the oxygen on these same density surfaces is lower. After January the CU decreases in strength and deepens, and by March it disappears in many locations, at least with respect to the assumption of zero flow at 500 dbar. (This assumption requires testing in the vicinity of the continental slope.) This deepening of the CU coincides with the return of persistent northwesterly winds. Thus the CU, which likely has a nonlocal density-driven component of forcing, surfaces and becomes the IC during periods of minimum surface wind forcing (October to February). During periods of maximum wind forcing (March to August), inshore surface equatorward flow overlies the CU.

5.4. *Seasonal Differences: Vertical Sections*

Seasonal variability in the strength of baroclinic flow changes the distribution of characteristics in the water column in two ways: (1) through the local vertical readjustment of the water column to a time-varying baroclinic field and (2) through time-varying lateral transport of nonlocal waters with different characteristics (i.e., with lateral gradients in T, S, and O_2). A vertical section of the difference in σ_t between mid-January and mid-July for line 90 (Figure 16) coupled with characteristic curves (Figure 17) illustrates this point. The decrease of σ_t in the surface layer (upper 25 to 50 m) from January to July

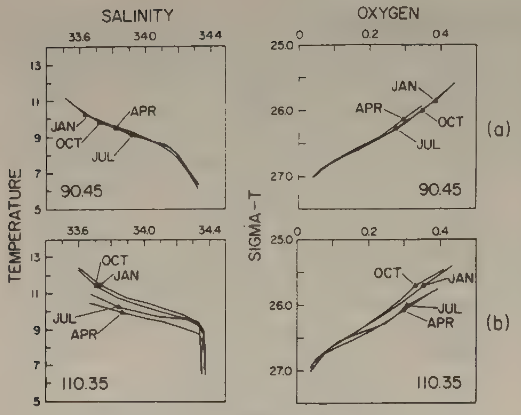

Fig. 17. Temperature versus salinity and oxygen versus σ_t for stations 90.45 and 110.35. Plots are given for January, April, July, and October. Values are plotted for depths of 75–500 m. The values at 100 m are marked by solid triangles for each month.

reflects the local seasonal warming. (The corresponding increase in surface temperature is 1.2° to 4.8°C.) Between the coast and station 70 and below 30 m there is an increase of σ_t over this period that reflects the change in the density field associated with the spin-up of the Southern California Eddy. The doming in the density field is also seen as a large negative anomaly in oxygen (Figure 16*b*) and negative and positive anomalies in the fields of temperature and salinity, respectively (not shown). That the local vertical readjustment to a seasonally varying geostrophic velocity field explains the greater part of the seasonal change in characteristics is evident in station plots (for 75 m and deeper) of temperature versus salinity and oxygen versus density (Figure 17*a*). The temperature versus salinity and oxygen versus σ_t curves for station 90.45 are very nearly seasonally invariant. The indications of the 100-m level on these four "seasonal" plots, however, demonstrate that there is a strong seasonal variation at this level. It is the local vertical readjustment of the water column to the seasonally varying flow field that produces changes at this and other levels. Station 90.45 lies near the center of the Southern California Eddy.

At other stations there is a significant seasonal change in water mass characteristics that can account for a sizable portion of the overall variation at depth. Many of these stations are located along the coastal margin. As an example, at station 110.35 (Figure 17*b*), the seasonal range of differences in *T-S* and O_2-σ_t curves is of the same order as the range for the sample depth given in the figure. This station is found close against the continental slope and in a region where there is a strong and varying surface (Plate 1) and subsurface flow (Figure 12). The northward penetration of warm, saline, low-oxygen water along the coastal margin is seen to extend and withdraw in the series of distributions on the 26.6-σ_t surface (Plate 2).

The time of occurrence of the maximum in σ_t versus depth and distance offshore from central to Baja California falls into simple patterns (Figure 18). In the surface layer the maximum occurs in late winter as a consequence of seasonal cooling. There is abrupt change below the surface layer in the offshore region, shown by a bold contour, where the maximum occurs in late summer and fall as a result of the vertical adjustment of the water column to a seasonal relaxation of the geostrophic flow of the CC. A vertical bold contour divides the offshore and nearshore zones. In the nearshore zone the maximum occurs in April–May, a period in which there is a spring transition characterized by a decrease or reversal of coastal poleward flow or a strong surge of equatorward flow. The stations nearest the vertical bold contours in Figure 18 (e.g., 70.60) often have a strong semiannual variation in the phasing of σ_t because of the interplay of the nearshore and offshore events. This narrow zone where the density field pivots on a horizontal axis coincides with the transition zone between coastal and oceanic regimes defined by the field of dynamic height (Figure 4). The phasing found at station 110.120 (Figure 18) appears to be a singularity (see also Figure 4*c*) and may be the result of inadequate sampling (15 observations).

The opposite phase of this σ_t cycle is not as coherent; the minimum in σ_t does not form such a simple set of patterns. A decrease in σ_t occurs in the surface layer in late summer as a result of seasonal warming and also at depth in winter along the coast as a result of the local adjustment of σ_t to the seasonally varying poleward CU flow. The peak velocities of the CU, however, occur over an extended period, and in some regions there are two

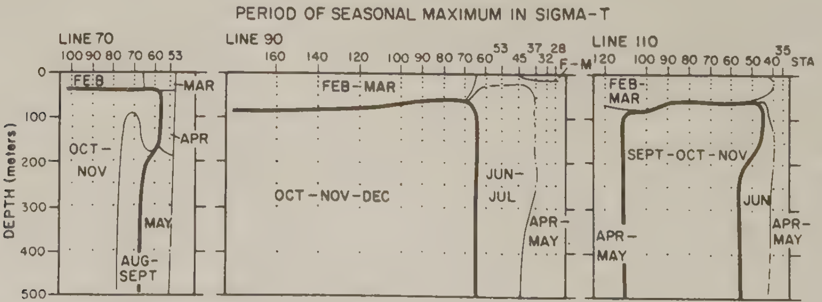

Fig. 18. Vertical sections showing the months of the seasonal maximum in σ_t for CalCOFI lines 70, 90, and 110. The heavy contour denotes a temporal discontinuity.

such periods. Thus the phasing of the seasonal minimum in σ_t is less well structured.

5.5. *Regional Differences*

The sets of characteristics at each of the cardinal lines often reveal regional peculiarities. For instance, line 70 is well situated to show events typical of the very nearly straight coastline of central California along which there are frequent northwest winds parallel to the coast and strong upwelling. Line 80, 220 km to the south, lies off a point of land where there is a major reorientation of the coastline. A coastal undercurrent and/or surface counterflow about this point intermittently disrupts the local effects of upwelling, and hence the patterns of temperature and oxygen differ from the regions to the north. Line 90 bisects the Southern California Bight and its offshore banks. These bathymetric features create their own signature in the distributions. Line 100 lies in a region where either there is an onshore limb of the Southern California Eddy or an intensified CC pressed against the coast. The record at line 110 provides a more consistent picture of the intensified flow along the coast of northern Baja California. Line 120 lies slightly northeast of Punta Eugenia, the most prominent projection of land in the study area. This station line lies in the northern limb of a large cyclonic eddy that intensifies seasonally. Line 130, which lies off a large bight, is rather lightly sampled for the complex frontal events evident there. Cardinal lines 70, 90, and 110 are the most suitable as representative examples of large regions of the generalized southeast-northwest flow patterns; flow is mostly perpendicular to these lines.

6. CONCLUSIONS

The seasonal variation of the physical characteristics and large-scale current patterns of the California Current system are examined using harmonic analysis applied to the 1950–1978 CalCOFI data set. The study covered the California Current system from the coast to approximately 1000 km offshore and from San Francisco to Baja California. The major conclusions of this study are as follows:

1. There are three domains; oceanic, coastal, and an intervening transition zone, defined by the amplitude and phasing of the seasonal variation of the dynamic height and by the standard deviation of the overall record of dynamic height. Dynamic height in the oceanic domain is controlled by large-scale air-sea interaction processes and large-scale dynamics. In the coastal domain it is dominated by alterations in the inshore surface and subsurface current structure. In the transition zone, variations of dynamic height are dominated by nonseasonal events: offshore mesoscale eddies and meanders in the high-speed core of the California Current.

2. The California Current is primarily an offshore, near-surface (0–300 m) equatorward flow whose core is characterized by low salinities and low temperatures. Off central and southern California the core of the CC usually occurs 300 to 400 km offshore, and off Baja California it occurs within 200 km of the coast.

3. The region of the low-salinity, high geostrophic velocity core also corresponds to the eddy-dominated transition zone.

4. Distribution of characteristics shows that there is a strong interaction between the core of the CC and the mesoscale eddy field.

5. The seasonal cycle of flow within the California Current system is characterized by the seasonal appearance of the Inshore Countercurrent and the Southern California Eddy and by the intensification of the California Undercurrent. Evidence suggests that the fall–winter appearance of the IC is associated with the shoaling of the CU.

6. The strong semiannual oscillation of the IC and CU in the Southern California Bight and regions farther north may be related to the seasonal development of the Southern California Eddy.

7. Below the surface layer (or upper thermocline) the seasonal variation of water mass characteristics is related to both the vertical adjustment of the water column to seasonally varying geostrophic currents and to varying transport of waters from different sources.

8. At depths of the CU core there is a seasonal variation in the water mass characteristics that is associated with the variation in the strength of the flow.

9. There is a strong coherent pattern in phasing of σ_t with depth and distance offshore. The transition zone, as defined by the statistics of the dynamic height field, has vertical extent as evidenced by the lateral discontinuity in the pattern of σ_t phasing.

10. The vertical discontinuity in σ_t phasing shows that below about 100 m, seasonal variation in density is controlled largely by dynamic processes. Above 100 m, however, thermodynamic processes also are important.

Acknowledgments. This study would not have been possible without the extensive efforts that many dedicated individuals have contributed to the long-standing CalCOFI program. The large archive of physical oceanographic data is a data set that is unique in so many ways, especially in its high level of quality and its spatial and temporal coverage. We wish to express our thanks to L. Eber for providing the data file and assisting in its manipulation, to S. McBride for typing the many versions of our manuscript, and to N. Hulbirt and G. Tapper for drafting the figures. Partial financial support was provided to J.J.S. by the Marine Life Research Group of the Scripps Institution of Oceanography, the California Space Institute, and the Office of Naval Research under contract N00014-86-K-0752.

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